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THE BENTHIC ECOLOGY OF FALSE BAY

PART I: THE BIOLOGY OF INFRATIDAL ROCKS, OBSERVED BY DIVING, RELATED TO THAT OF INTERTIDAL ROCKS

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(Communicated by J. H. DAY)

(With eleven text-figures and Plates XIX-XXII)

(Read November 20, 1957)

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INTRODUCTION

The vast and growing literature on benthic ecology divides rather sharply into papers concerning the intertidal region and those dealing with the sea-bed. The division follows a difference in accessibility for workers have tended to follow field-methods that are familiar to them. Thus, those interested in the intertidal region have problems that involve direct observation and direct manual work; they see their work and walk amongst it. But those tackling the sea-bed usually cannot see it nor approach it personally. The techniques in these fields unfortunately do not overlap but, on the contrary, become increasingly difficult at the lowest tidal levels for the intertidal ecologist and in shallow water for the submarine ecologist. The result is not only a gap in our knowledge but an artificial differentiation between the ecology of the two regions.

Many have been unhappy about this. Filling the gap has depended on special methods and on biologists willing to use them. As long ago as 1844, H. Milne-Edwards used a diving-suit for personal observation underwater, and several naturalists have done so since, including Gislén (1929 and 1930), who specifically attempted to treat the intertidal and infratidal uniformly. Despite the paucity of work in the shallows, Ekman (1935, revised 1952) grouped the biota of the intertidal region together with that extending downwards from it to the edge of the continental shelf; Gislén (1944) adopted the same grouping. Both recognized the biotic continuity despite the gap in knowledge.

Knowledge is now being rapidly increased by use of more suitable methods than conventional diving. Revival of the diving-hood by Beebe (1926) has brought an inexpensive method to light. It has been used very successfully by him and by Kitching, Macan and Gilson (1934), and Kitching (1941), for example. Recently a revolutionary improvement in access to the shallows occurred with the perfection of the self-contained diving apparatus (pointed out by Drach, 1948a and 1952). After using this method, Drach gives some general biological observations on the shallows (1948b) and on the constitution of Laminarian beds (1949). And in England Forster (1954 and 1955) has published notes on the biota of rocks down to over 25 m. depth.

It is to be hoped that the new impetus given by the self-contained diving apparatus to the study of the shallows will not result in a third, unrelated body of knowledge but that intertidal ecology will be linked to that of deeper water. In this work in False Bay particular attention has been paid to the shallows, the ecology of which has been linked with that of the intertidal region (in this paper) and with dredged bottoms (in Part II). Of necessity field-methods differed but they were overlapped to achieve as consecutive a story as possible of biotic changes from the intertidal region to about 90 m. depth.

So far as intertidal rocks are concerned, South Africa is fortunate in having the brilliant survey by Stephenson (1939, 1944, 1947) and colleagues. Below tidal levels there is a fair amount of information from dredging on the shelf but it is scattered and only Ekman has really made any synthesis of it. There has been no work in this country correlating intertidal with infratidal ecology. Since the intertidal is well

known, emphasis here is on the infratidal. In this paper the biotas of the rocks of the two regions are compared at one locality and descriptions are given of deeper rocks found elsewhere to a maximum depth of 17 m. Detailed collections were made of the species at any height above low-tide level or depth below it in an effort to determine their depth ranges within narrow limits so that the transition from the intertidal to the infratidal could be analysed by the method of critical levels (Colman, 1933). This elucidated the question of the affinities of the 'sublittoral fringe' of Stephenson. Several species new to science have resulted incidentally.

It would have been logical to make this comparison at one of the stations described in detail in the Stephenson survey such as St. James, in False Bay, described by Eyre (1939). But St. James is unsuitable for diving due to the shallowness of the water and the amount of surf there, and consequent water turbidity. The place finally chosen for diving, Oatland Point, differs from St. James in important respects as will be shown later. Unfortunately my intertidal results at Oatland Point cannot be compared with those of Eyre to elucidate these differences because her description of the St. James locality almost certainly includes small pools and crevices and the biota of the different levels of the shore are not distinguished in great detail.

It is necessary to define clearly the terminology used here. In the Stephenson survey series of papers (fully listed in Stephenson, 1947) the intertidal region was called the 'intertidal' and was subdivided into horizontal biotic zones. Below the level of Extreme Low Water of Spring Tides (E.L.W.S.) was termed the 'sublittoral' (Stephenson, 1939) and from E.L.W.S. upwards for a variable extent but approximately to the mean level of Low Water of Spring Tides (M.L.W.S.) was termed the 'sublittoral fringe'. Later, Stephenson and Stephenson (1949) replaced the word 'intertidal' with 'littoral' and 'sublittoral' with 'infralittoral' despite previous criticisms of the debasement of the word 'littoral'. Similar criticisms of the word 'littoral' have been made by Ekman: in 1935 he used it to mean the area from the top of the intertidal region down to the edge of the continental shelf but replaced it by the term 'shelf fauna' in 1952. Gislen (1944) uses the term 'sanidal', corresponding to Ekman's 'shelf fauna', in an effort to avoid the word 'littoral'. Day, Millard and Harrison (1952) also shun 'littoral' and point out that the term 'intertidal zone' for the region of the shore between tide marks is widely accepted. They suggest that the fringe of the sea-bed below the intertidal zone be referred to as the 'infratidal fringe', this term replacing both 'sublittoral fringe' and 'infralittoral fringe'. The term implies that the region of the sea never bared by tides be called the 'infratidal zone' although they do not say this in so many words.

ENVIRONMENTAL NOTES

A. GEOGRAPHICAL

False Bay is a well-defined bay of the sea roughly square in shape and open to the south, the sides being about 20 miles long (fig. 1). The bay is about 12 miles south of Cape Town and is separated from the South Atlantic by the Cape Peninsula which is the westerly limit of the southern coast of Africa. The bay cannot be

regarded as having any estuarine characteristics for it is large and has negligible fresh-water inflow. No large rivers enter the bay but in winter there are many mountain streams on the westerly and easterly shores, two of which on the easterly side are dignified with the title of river, the Steenbras River and the Rooi Els River. The mouth of the bay is too large for it to have characteristics of a marine lagoon. False Bay is best regarded as part of the oceanic coastline where there is some shelter from the full effects of swell and storm, particularly in winter.

The place selected for most of the work was Oatland Point as being easily accessible by road and the nearest place suitable for diving. Figure 1 shows that Oatland Point is the nearest place where the bottom slopes appreciably. It provides reasonably deep and clear water and very varied rock faces. The ground slopes to the sea without streams near by. At the water's edge are granite formations forming almost horizontal pavements and vertical walls. Splits in the large masses may form V-shaped clefts between cubiform slabs. Erosion forms characteristically rounded boulders lying next to, and on top of, one another with ramifying crevices and increased erosion at the bases of the boulders forms small hollows and large caves. The rock formation is similar both above and below water.

Oatland Point continues seaward as many separate large rocks rising abruptly from the bottom. At low tide a distinct, shallow lagoon is formed by a semi-circle of rocks through which the water passes freely only at the north and south. (Sketch map, fig. 2.) The Lagoon is D-shaped, roughly 50 metres long, 40 metres wide and 1-2 metres deep at L.W.S.T. A conspicuous, large rock at the middle of its periphery is named 'Lagoon Rock'. Most of the rocks in the Lagoon are covered at M.H.W.S. but the outer semi-circle remains exposed and gives considerable protection from the swell.

Outside the Lagoon a scattered series of rocks forms a discontinuous outer semi-circle. The northern part of the gap between the two semi-circles is named 'The Channel' and is about 60 metres long, 30 metres broad and 6 metres deep at L.W.S.T. Usually there are currents through it due to tide and wind. A conspicuous large rock of the outer semi-circle is called 'Big Rock'; it lies seaward of Lagoon Rock and is separated from it by the southern end of the Channel. Seaward of the outer semicircle the bottom is sandy and slopes gently away from a depth of about 8 metres.

Diving was not confined to Oatland Point. Deeper rocks were found elsewhere, namely at Roman Rock Lighthouse (fig. 1), at Noah's Ark and the Quay, Gordon's Bay Harbour. Further details of the places at which collections were made will be given with the biological descriptions.

Unfortunately the intertidal and infratidal could not be examined on the same rocks because suitable ones were rare and inaccessible. It was decided that four intertidal transects were desirable to show different degrees of exposure to wave action. Three faces were selected at Oatland Point, but one that was very exposed to swell and at the same time accessible could not be found nearer than Froggy Pond which is the nearest point to the north, only 400 metres distant. It is too close to be distinguished in figure 1.

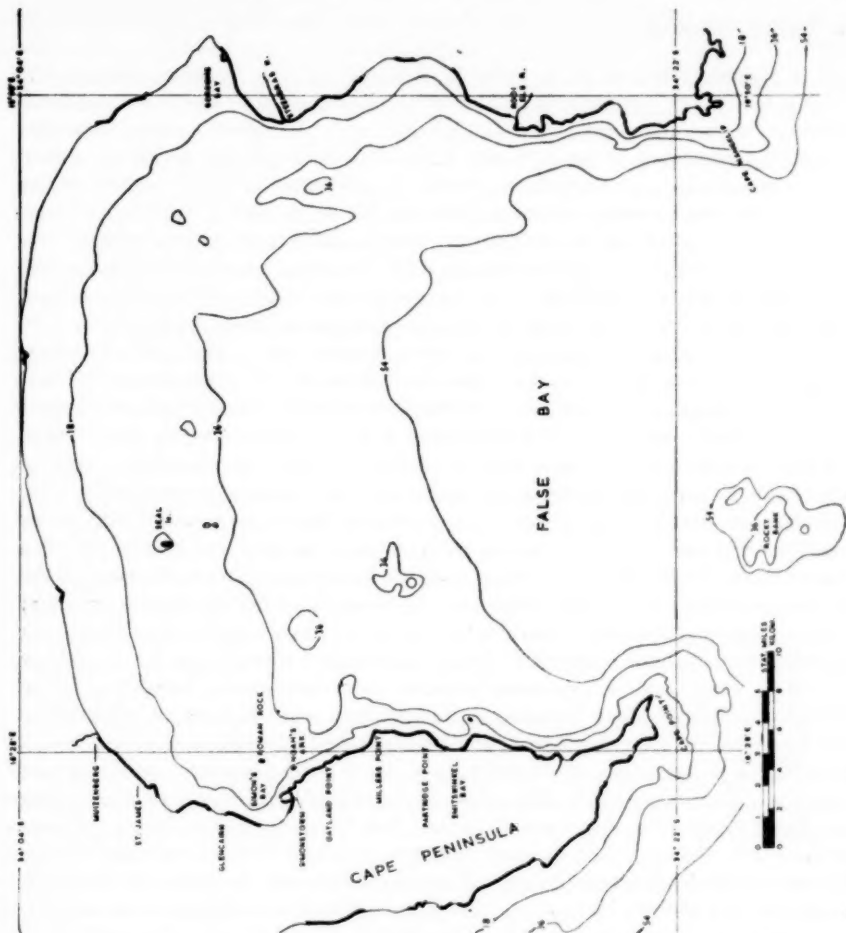


FIG. 1. *False Bay*.
Based on British Admiralty chart
696.
Sandy shores in thin line, rocky
shores in thick line.
Depth in metres: the contours
approximate to those at 10, 20
and 30 fathoms.

Based on British Admiralty chart
636.

Sandy shores in thin line, rocky shores in thick line.

Depth in metres: the contours approximate to those at 10, 20 and 30 fathoms.

B. PHYSICO-CHEMICAL

According to Ekman (1952) False Bay lies in the 'Warm-Temperate Region' but Stephenson (1947), commenting on Ekman's 1935 edition, notes that it is transitional between 'Warm-Temperate' and 'Cold-Temperate'. Stephenson (1944) describes the main components of the intertidal rocky biota of South Africa. He recognizes three main components, correlated chiefly to hydrographic factors: those of the western, southern and eastern coasts. False Bay lies in the region of overlap between Stephenson's western and southern components. The mixed hydrographical conditions of the overlap are further complicated by peculiarities within the bay, as will be mentioned below. Stephenson (1944) devotes a section to the Cape Peninsula, and states that the whole of his survey arose from a desire to elucidate the problems of the Cape Peninsula itself. He suggests that in the 17 miles from Cape Point to Muizenberg changes occur similar to those from Cape Point to 100 miles eastward of it.

The hydrography of False Bay is undeniably complex and has not been worked out even approximately, but full knowledge is not necessary for this paper. It is sufficient to note that from Cape Point to Muizenberg there are remarkable, obvious changes in the intertidal flora and fauna, changes which Stephenson has shown to be correlated eastwards along the coastline of southern Africa with marked changes in the characteristics of the water masses, particularly in temperature. In discussing this matter again, Stephenson (1947, fig. 7) gives the hourly variations in sea temperature at various localities on one particular day: St. James shows the highest temperatures; those at Miller's Point, some 8 miles to the south, are about 3° C. lower. These data are suggestive but not conclusive. Many unpublished observations by the author over three years confirm Stephenson's comments on temperature variability. They show that, although there is usually no temperature gradient between Muizenberg and Cape Point when the year as a whole is considered, any temperature gradient is from higher temperatures at Muizenberg to lower temperatures to the south and that this is a summer feature. The cause of the gradient is presumably the prevailing south-east wind of summer which causes drift of warm surface water towards Muizenberg. Figures could be produced from available data to prove almost any hypothetical hydrographical arrangement in False Bay but Stephenson's figures for St. James and Miller's Point give likely 'typical summer conditions' of water temperature along this coastline. In winter there is unlikely to be a north-south temperature gradient because the wind blows from the north-west and the effect of sunshine is less.

Some indication of the yearly temperature cycle of surface water in False Bay is given in figure 3. The curve for St. James is for 1930 (Marchand, 1932); those for Muizenberg and Roman Rock (in Simon's Bay) are derived from Isaac (1937) who does not state over what years the data were averaged. Muizenberg and St. James are near by and so the differences between their curves are presumably due to the data having been drawn from different years. But it should be valid to compare the curves for Muizenberg and Roman Rock and they show temperatures at Roman Rock to be lower, usually. One cannot say whether this is part of the

north-south gradient mentioned or whether it is due to Roman Rock being offshore, with some 17 metres depth of water immediately around it.

So far as the yearly cycle at Oatland Point is concerned the author took numerous temperature readings but it was impossible to do so systematically. This fact, together with the fact that temperatures in any month could vary greatly from year to year, renders the figures unsuitable for comparison with figure 3. For example, in March 1953 the mean of four readings was 18.7°C ., and in March 1954 the mean of five readings was 15.9°C . However, the main features of these records are summarized in Table I for comparison with Marchand's data for St. James in 1930. The average monthly temperatures for Oatland Point over two and a quarter years are the same as those for St. James back in 1930, but St. James appeared to have greater extremes.

In September 1953 four stations in False Bay, a few miles offshore, were sampled hydrologically as will be discussed in detail in another paper, relative to dredging work. It is sufficient to state here that from 0 to 20 metres depth both temperatures and salinities were found to vary only very slightly with depth. But diving experience showed that vertical temperature gradients were the rule rather than the exception, certainly in summer, and this is confirmed by the records of two occasions when underwater temperatures were taken by manual operation of a reversing thermometer. In November 1953 the surface temperature of the Lagoon at Oatland Point was 17.4°C . and that on the bottom (2 m. below) was 17.2°C . On the same date the temperature of the surface of the Channel was 17.4°C . and that on the bottom (6 m. below) was 15.2°C . The wind was fresh south-easterly. As a result of diving, it is suggested that temperatures at 15 metres depth are $2-4^{\circ}\text{C}$. lower than those on the surface: this applies only to the north-west of False Bay, where most diving was done in summer.

Marchand gives figures for the daily variation in hydrogen ion concentration at St. James in 1930 and a graph of the monthly means which are summarized here in Table I. It will be seen that there is a marked seasonal variation: Marchand couples the high summer pH with a dense phytoplankton population and the consequent assimilation of CO_2 from the water. It should be noted that there are no dense algal beds at St. James to affect the inshore values markedly.

In January 1928, Hogben and Zoond (1928) investigated the surface hydrogen ion concentration from about 2 miles off Partridge Point (fig. 1) around the Cape Peninsula to Table Bay. They found no statistically significant difference between the pH of waters on either side of the Peninsula although two markedly different bodies of water were sampled, differing in temperature by over 5°C . Thus it would seem likely that the bulk of the surface water of False Bay shows little variation in pH. Even so, a gradient from Cape Point to Muizenberg might exist at the water's edge due, not to hydrographical features, but to the presence of great kelp beds in the south and the meagre algal growth in the north. This possibility has not been investigated.

False Bay appears to be a mixture of waters derived from various sources and then agitated by the wind, deflected according to topography and warmed by the sun. Marchand points out that the salinity curve for 1930 at St. James closely

ST. JAMES 1930						
	OATLAND POINT 7.6.52 to 29.9.54	Random daytime sea surface temperatures	Regular daytime sea surface temperatures	Regular noon sea surface pH values	Regular noon sea surface salinity	Regular daytime air (dry) temperatures
Average of Monthly Means	16.3° C.		16.3° C.	8.16	35.31‰	18.9° C.
	—		18.3° C. (Jan. & Nov.)	8.50 (Feb.)	35.65‰ (Jan.)	24° C. (Jan.)
Monthly Means	—		13.3° C. (Aug.)	7.75 (July)	35.05‰ (June & July)	14° C. (July & Aug.)
	20.3° C. (March 1953)		21.2° C. (Feb.)	8.55 (Jan.)	36.66‰ (Jan.)	25.4° C. (Jan.)
Extremes recorded	13.3° C. (May 1953)		11.9° C. (Aug.)	7.68 (July)	34.99‰ (July)	10.6° C. (Aug.)

TABLE I

Conditions at the water's edge on the west coast of False Bay
(Data for St. James derived from Marchand, 1932)

follows that of sea temperature, and also that the air temperature curve is of the same type as the sea temperature curve but exaggerated, being only just higher in winter but markedly higher in summer. The chief features of these data are entered here in Table I for convenience. Hogben and Zoond suggest that, in general, differences in pH, dissolved oxygen and salinity are unimportant as factors governing local distribution of marine species but that temperature is very important.

In a consideration of possible differences along the west coast of False Bay, mention of wave action and the nature of the substratum must be mentioned. Swell is usual in the bay but can only enter from the south. It diminishes as it progresses northwards and produces rollers and surf over the shelving sea-bed, particularly in the north. The coast is not greatly indented and very sheltered localities are rare. Most of this coast is rocky. A centre section, from Simonstown to Smitswinkel Bay (fig. 1) is of Pre-Cape granite but most of the rest consists of Table Mountain Sandstone with small granite outcrops. The granite characteristically forms islands and chains of rounded, giant rocks such as those at Oatland Point whereas the sandstone usually lies in flat terraces as at St. James. Of course, both occur in the jumble of rounded boulders at low-tide level.

A. METHODS

INTERTIDAL BIOLOGY

Since the chief characteristic of the intertidal zone is intermittent exposure to air, it was decided that pools and crevices should be avoided. With this in mind, four intertidal sites were chosen which differed in exposure to wave action.

It was decided that biotic levels should be related to absolute levels rather than to tidal ones, and for this purpose a datum had to be chosen from several that could be considered. The datum adopted was that of the South African Railways and Harbours tide gauge in Cape Town harbour; this datum is said to be at 'L.W.O.S.T.' level (or M.L.W.S.) for Table Bay. The work of Bokenham, Neugebauer and Stephenson (1938) on tidal levels in False Bay is commented upon below but it must be mentioned here that they found M.L.W.S. at Simonstown to be about $3\frac{1}{2}$ inches below the datum of the Cape Town harbour gauge (Table II). In this series of papers, all heights and depths are measured from this datum which, by definition, divides the intertidal from the infratidal zone. Unusually low spring tides will expose part of the infratidal zone and this region is termed 'the infratidal fringe'. These definitions correspond closely to the terms used by Stephenson (1939 etc.). It must be remembered that the terms 'datum level' and 'M.L.W.S. level' are not quite synonymous in False Bay but the difference is negligible for most purposes.

At each site, a position was taken as a bench mark and the levels of conspicuous biotic features were related to it by a method suggested by Professor Day. The method involves two workers, each with an 8-foot surveyor's ranging rod. The rods are stood vertically on the two points which are to be surveyed and, with the eye close to a convenient height on the one rod, a sight is taken looking past the other rod towards the horizon. This sight is reckoned to be horizontal. A slide is moved along the second rod until its top intersects the line of sight. The difference between the

level of the eye of the viewer and that of the top of the slide gives the change in level of the substratum. Where a natural horizon is not available an Abney level provides an artificial one. Levels could be measured to a probable accuracy of ± 0.25 inches over distances up to 30 feet.

The bench marks of the transects were surveyed professionally in relation to Trigonometrical Survey bench mark number 436 to an accuracy of ± 0.02 feet. I am informed by the Director of the Trigonometrical Survey that 'all height values for bench marks in the vicinity of Cape Town are referred to M.S.L. Cape Town' which the S.A.R. and H. authorities in Cape Town inform me is 2.224 English feet above the tide-gauge datum. Transect levels have been correspondingly altered to read as from the datum adopted here and converted to the metric scale.

	Relative to Trigonometrical Survey datum ("M.S.L.") in feet	Conversion relative to Cape Town tide gauge datum (M.L.W.S.) in inches	Conversion relative to Cape Town tide gauge datum (M.L.W.S.) in metres
E.H.W.S.	3.68	70.85	1.80
M.H.W.S.	2.92	61.73	1.57
M.H.W.N.	0.73	35.46	0.90
M.L.W.N.	-0.38	22.12	0.56
M.L.W.S.	-2.52	- 3.55	-0.09
E.L.W.S.	-3.32	-13.15	-0.33

TABLE II. Tidal levels at Simonstown
(Based on Bokenham, Neugebauer and Stephenson, 1938.)

Tidal levels have been calculated for Simonstown by Bokenham *et al.* on the basis of tide-gauge traces there for 1933-5. Levels have been given (p. 117 of their paper) relative to 'Mean Sea Level' which Dr. N. A. H. Millard (née Bokenham) tells me is the same level as that used as reference by the Trigonometrical Survey. These tidal levels are quoted here for convenience (Table II) with conversions to the datum used in this paper and to the metric scale.

The definitions of the tidal levels used by Bokenham *et al.* are worth noting, particularly their comment on the difficulty in determining the levels of extreme neap tides due to the highest low water not falling as low as the lowest high water recorded.

OATLAND POINT			FROGGY POND
Sheltered Rock	Northern Lagoon Ramp	Beacon Ramp	
<i>Shady, very sheltered</i>	<i>Sheltered</i>	<i>Semi-exposed</i>	<i>Exposed</i>
0.30 m.	0.46 m.	1.02 m.	1.68 m.
0.38	0.49	0.85	0.99
0.38	(0.28)	1.19	1.55
0.33	(0.17)	0.36	0.70

TABLE III

Vertical wash ranges on four occasions at the selected intertidal sites. Values in brackets are low because they were obtained at low tide when the site became extra sheltered by emergent rocks.

The more exposed a rock is to wave action, the greater the difference between the levels of wave upwash and suck-back upon it, and this difference may be termed the 'wash range'. If we compare the wash ranges at the selected intertidal sites we should get an idea of their relative exposure to wave action, although, strictly speaking, the comparison should be made between rocks of identical slope.

Wash ranges were noted on four occasions and are tabulated in Table III. In three sites exposure to wave action did not depend on tidal level, but one, Northern Lagoon Ramp, gained increased shelter below half tide level from emergent rocks to seaward. There is progressive increase in wash range from Sheltered Rock to Froggy Pond. Experience suggests that the first line of Table III represents normal conditions. Table III includes a verbal description of the exposure to wave action at each site and hereafter the sites will be designated by these descriptions.

It is felt that about three-quarters of the wash range represents upwash above actual tidal level and one-quarter represents suck-back below it because suck-back is minimized by water cascading from the rock. It may be argued that upwash is more important to the biota than suck-back and that tidal levels are effectively raised by the height of the upwash.

As has been mentioned, sites were chosen that did not have deep crevices or pools. At each site, there were horizontal changes in biota due to local rock formation and so the sites were only examined in detail along vertical transects about 2 metres wide. Detailed field-notes were made of the conspicuous species in relation to surveyed levels and collections were taken from all levels for laboratory sorting of small species. The method of examination used by Evans (1947) was not adopted because the areas of the sites were small and because detailed collections were desired.

B. THE BIOTA

(i) *Shady, Very Sheltered Site* ('Sheltered Rock', fig. 2)

Upwash 0.23 m. (9 in.).

The transect faced south but backed upon the sea and so was maximally protected from wave action. Since it was overhanging the transect was always shaded and near-by rocks increased the dimness of illumination.

The rock under consideration rested on a great granite slab just below datum level. The transect lay on the underside of a face sloping at about 40° to the horizontal and running straight from below datum to about 1.6 m. height (i.e. M.H.W.S. level) above which it curved past the vertical (fig. 4).

The biota was typical of similar situations near by, although not so crypto-faunistic in nature as smaller and more inaccessible places. The face was brightly coloured at lowest levels with anemones (*Bunodosoma capensis*), with various sponges (e.g. *?Geodia littoralis*, catalogue number CP.426 B, and *?Hymeniacidon perlevis* CP.426 C) and with the ascidian *Amaroucium ?erythraeum* (CP.428 B). The soft polychaete, *Menipea crista*, was common among them and there were fair numbers of *Balanus trigonus* and occasional small *Mytilus crenatus*. The sponges and anemones and *Menipea* were replaced by a dense growth of the barnacle *Octomeris angulosus* which flourished from 0.2 m. height to M.H.W.N. level and, in the lower half of this range,

i.e. below M.L.W.N., completely dominated the rock. A dusty looking '*Lithothamnion*' was common on *Octomeris*, particularly in the upper half of the range of the barnacle. Above M.L.W.N. level, the serpulid worm, *Pomatoleios kraussii*, progressively took more space at the expense of the barnacle and its tubes supported the only soft alga that was present in fair quantity, namely the tiny, red *Pleonosporium harveyanum*. The barnacle *Octomeris* dwindled to extinction above M.H.W.N. level and the upper limit of *Pomatoleios* was at the same level but was very sharply defined. The barnacles *Tetracrita serrata* and, in lesser abundance, *Chthamalus dentatus* started to appear below this conspicious line but only became very abundant above it where they dominated the rock almost to M.H.W.S. level.

Only a few mobile species were to be found, namely *Asterina exigua* and *Henricia ornata* at low levels, *Patella granularis* and *Oxystele variegata* among the *Tetracrita*, and a few *Littorina knysnaensis* above all other species. Of these only *P. granularis* was common. The upper limits of *Tetracrita*, *Chthamalus* and *P. granularis* made a rather well-marked line about 0.2 metre below M.H.W.S. level.

Stephenson (1939 etc.) has firmly established terminology for zonation on intertidal rocks in South Africa. On this site the lower limit of Stephenson's Littorina zone is clearly at the upper limits of *Tetracrita*, *Chthamalus* and *P. granularis* (just below M.H.W.S. level). These three species are virtually the only occupants of the Upper Balanoid zone. The upper limit of *Pomatoleios*, just above M.H.W.N. level, provides another clear demarcation line, this time between Upper and Lower Balanoid zones. There is no Cochlear zone and so the Lower Balanoid zone here merges imperceptibly at about datum level into Stephenson's 'Sublittoral fringe' (the quotation marks are inserted to show that the term is not accepted in this paper).

(ii) *Sheltered Site* ('Northern Lagoon Ramp', fig. 2)

Upwash 0.34 m. (1 ft. 1½ in.) above half tide level and much less lower down.

The transect faced SSW. so swell or surf did not smack directly on to it but ran across the transect.

The rock face rose vertically from about one metre depth to a step situated a little above datum. The step was about 0.3 metre wide and above it the face rose vertically again to the height of 1.6 metres where it flattened rather sharply (fig. 4).

In the infratidal zone the kelp *Ecklonia maxima* flourished although most of the rock was colonized by a smooth, thick, crusty '*Lithothamnion*' (CP.392 B) upon which little grew.

Ecklonia and crusty '*Lithothamnion*' rose a little above datum but the kelp was very small intertidally. There was a sharp transition to a well-developed but narrow band of the gastropod *Vermetus corallinaceus*, which was replaced by the worm *Pomatoleios* higher up. The upper limit of *Pomatoleios* occurred here just above M.L.W.N. level and was also rather sharp; above it the grey barnacle *Tetracrita* dominated the rock to M.H.W.S. level with *Chthamalus* present in smaller numbers. Dusty '*Lithothamnion*' usually colonized both the *Vermetus* and the *Pomatoleios* tubes. The tufted alga *Gelidium pristoides* made a frilly, narrow line at the *Vermetus*/*Pomatoleios* overlap and there were a few *Iridophycus* plants above it.

There were very few mobile species present. *Acanthochiton garnoti* was rather common among the *Pomatoleios* tubes but small *Patella granularis* and small *Oxystele variegata* were definitely commoner there and also higher up among the barnacles. *Littorina* invaded the highest barnacles from above.

In Stephenson's terminology the lower limit of the *Littorina* zone was just about at M.H.W.S. level, at the upper limits of *Tetracita*, *Chthamalus* and *P. granularis*. The Upper Balanoid zone gave way to the Lower at about M.S.L., the upper limit of *Pomatoleios*. The Cochlear zone was absent but was probably represented by the band of *Vermetus*; below this was the 'Sublittoral fringe' as represented by *Ecklonia* and the characteristic crusty '*Lithothamnion*'.

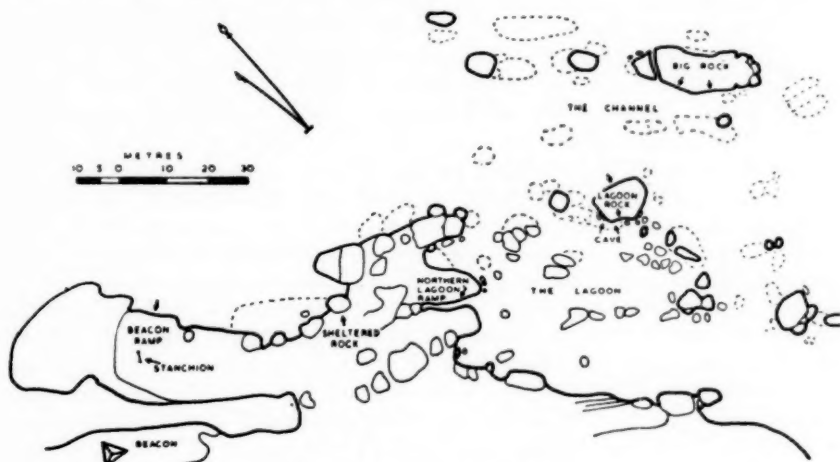


FIG. 2. Sketch map of Oatland Point

Main rock formations below datum are indicated by dashed lines. Arrows show places of work.

(iii) *Semi-exposed Site* ('Beacon Ramp', fig. 2)

Upwash 0.76 m. (2 ft. 6 in.).

The transect faced NE. and was protected from the direct force of the swell (SE. usually) but the latter veered round to impinge more on this site than might be supposed. The site faced the strong wind-induced chop that prevailed in winter.

Below the transect there was a stony bottom at about 1 m. depth from which the rock face rose vertically to datum and turned sharply to make a slope at about 60° to the horizontal. The slope undulated somewhat but at about 1 metre above datum it became progressively flatter until it was about horizontal at 1.8 m. height (fig. 4).

The two or three decimetres of vertical rock immediately above the bottom were almost devoid of soft algae and carried a biota similar to that on the stones of the adjacent bottom, i.e. '*Lithothamnion*' dominated and there were many *Parechinus angulosus*. Above this was a dense mat of tufty algae the commonest of which were

red *Dicurella flabellata*, green *Caulerpa filiformis* and olive *Dictyota dichotoma*. Others were common but varied from one year to another. For instance in September 1954 *Laurencia glomerata* and *Plocamium cornutum* were very common, but in March 1955 the former was absent at this level and only a few tufts of the latter were present. *Hypnea spicifera* and *Leathesia difformis* were fairly common, and *Ecklonia*, although common a few yards away, was represented by only occasional plants. On this infratidal face all the animals were small, the most conspicuous being the little pink anemone *Corynactis annulata* although there was a multitude of polychaetes and amphipods. A few small peach-coloured tunicates (CP.436 A, ? gen. et sp. nov.) were hidden among the algae.

In the intertidal zone the belt from M.L.W.S. to M.L.W.N. was dominated by a clearly demarcated zone of the limpet *Patella cochlear* and its associated 'Lithothamnion' and algal gardens and by the little serpulid *Spirorbis* n. sp. This site was richly populated with tufty algae and they particularly favoured the limpet shells. Some, such as *Ecklonia*, *Hypnea spicifera* and *Bifurcariopsis capensis*, rose from the intertidal to achieve their greatest growth just above M.L.W.S. Others grew densest around M.L.W.N., e.g. *Pterosiphonia cloiophylla* and the two tiny but common algae *Chyocladia capensis* and ?*Griffithsia* sp. (CP.396 F). *Gigartina radula* and *G. stiriata* were peculiar in that they flourished at two levels, i.e. just above M.L.W.S. and at M.L.W.N. with scanty plants in between. Some algae varied seasonally. In September 1954 *Laurencia glomerata* was common infratidally and rose as high as M.S.L. but in March 1955 it was less common and was restricted to the range occupied by *P. cochlear*. And on the former occasion *Plocamium cornutum* also extended from M.L.W.S. to M.S.L. but was absent from the transect six months later. Before leaving the lowest levels of the intertidal zone mention must be made of the tufty coralline algae that were numerous just above M.L.W.S. and which decreased in abundance higher up. And it must be pointed out that sessile animals were rare apart from *P. cochlear*. There were a few small anemones (*Bunodosoma*) and a few small *Mytilus crenatus* at and below M.L.W.N. level.

Clearly the lowest half of the intertidal zone is rich in species although most of them are rather small. The distribution of *P. cochlear*, and its associated 'Lithothamnion', ceased abruptly above M.L.W.N. and here, at the middle of the intertidal, was a rich but narrow belt of algae extending from among the limpets at M.L.W.N. to above M.H.W.N. level. The commonest were *Gelidium pristoides* and *Splachnidium rugosum* but *Aeodes orbitosa* was conspicuous a trifle lower than these. In this algal belt the barnacle *Octomeris* was common and small *Mytilus perna* fairly common, and both species were confined to it.

From M.H.W.N. to M.H.W.S. the rock was comparatively bare. The grey barnacle *Tetraclita* dominated the lower half with the small alga *Chaetangium ovale* thinly interspersed; the upper half was dominated by the tiny barnacle *Chthamalus*. In the lower range of *Chthamalus* there were patches of the alga *Porphyra* that replaced it.

The distribution of mobile animals on this transect rather depended on the shelter offered by algae. In the infratidal, *Oxystele sinensis* was sparsely dotted about but in the lower half of the intertidal it gathered under algal tufts and was scarcely to be

found in the open. Another gastropod commonly found beneath tufts was *Bernuapena cincta*. Above M.S.L. *O. sinensis* was replaced by the smaller *O. variegata* which, with *Patella granularis*, rose almost to M.H.W.S. level. *P. granularis* was found in the open spaces of the algal belt and among the *Tetracrita* above it but was absent above the *Tetracrita* except where *Porphyra* was present to shelter it. At the upper limit of *Tetracrita* a few *Littorina* were to be seen; they became common above M.H.W.S. and extended upwards to the highest level attained by the rock (2.08 m.).

This site showed all the typical zones as described by Stephenson. There is confusion in demarcating the *Littorina* from the Balanoid zone because *Porphyra*, which is typical of the *Littorina* zone, flourished here lower than the upper limit of *Chthamalus*. The upper limit of barnacles was rather sharp at M.H.W.S., the upper limit of *P. granularis*, Stephenson's alternative boundary line, was 0.1 metre lower and the lower limit of *Porphyra* was a further 0.2 metre lower.

The Upper and Lower Balanoid zones meet at the top of the algal belt, at M.H.W.N., and most of the Lower Balanoid zone is here replaced by the Cochlear zone. The Cochlear zone ends at M.L.W.S. and from M.L.W.S. to E.L.W.S. is clearly 'Sublittoral fringe' as represented by the algal mat which, as has been mentioned, started at M.L.W.S. and went down well into the infratidal.

(iv) *Exposed Site* (Froggy Pond, southernmost point)

The southern point of the bay at Froggy Pond was inaccessible; the site selected was the next point south of it.

Upwash 1.26 m. (4 ft. 1½ in.).

The transect faced ESE., almost in the eye of the swell. This point was also exposed to wind chop from the north caused by winter winds.

Below the transect there was a rocky bottom at about 1½ m. depth. From this, the rock rose almost vertically to just above datum where it became almost flat, forming a platform about 1½ metre wide. The face then rose at about 30° to a crest at M.H.W.S. level; above this it was ignored because of complicated rock shape (fig. 4).

The infratidal biota consisted of a motley assortment of species showing no clear or orderly arrangement. The alga *Dicurella fragilis* was commonest with pale '*Lithothamnion*', *Sargassum heterophyllum*, and small *Ecklonia* plants competing with each other for rock space, and with small specimens of the giant tunicate *Pyura stolonifera*. Numerous *Oxystele sinensis* and *Parechinus angulosus* were scattered around, the latter favouring niches in the rock.

The lower part of the intertidal zone was occupied by a well-developed mosaic of *P. cochlear* and its associated '*Lithothamnion*'. Their lower boundary was ill defined and, whereas the '*Lithothamnion*' went down to M.L.W.S. level, the limpets stopped about 0.2 metre above it. *Pyura* and a few algae such as *Dicurella fragilis*, *Sargassum heterophyllum* and *Ecklonia* rose from the infratidal to about M.L.W.N. A few others started at M.L.W.S. and rose to about M.S.L. but were insignificant in quantity (e.g. *Hypnea spicifera*). In September 1954 *Plocamium corallorhiza* and *Dicurella flabellata*

were common at low levels but were absent in March 1955. Tufts of algae were not an important feature of this site but, instead, protection was afforded to many small animals (polychaetes, amphipods and isopods) by numerous small clumps of *Balanus maxillaris* mixed with large *Octomeris* barnacles and small *Mytilus crenatus*.

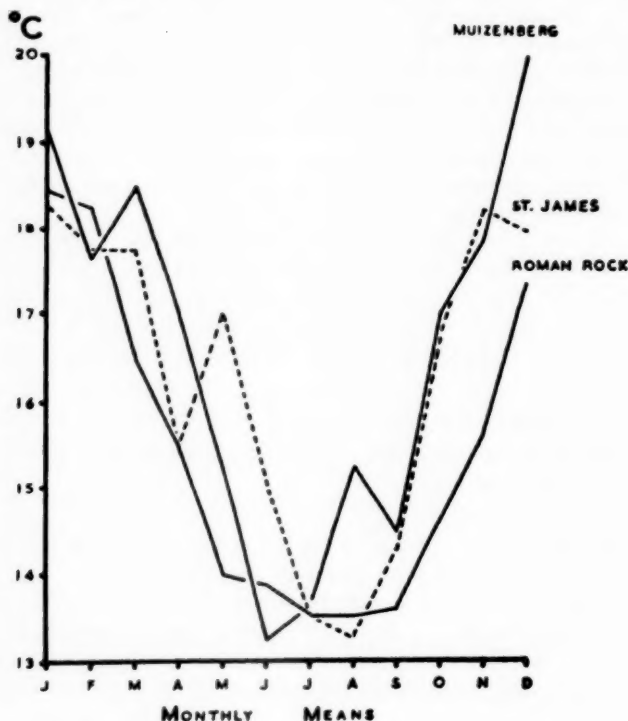


FIG. 3. Daytime temperatures of the surface of the sea in the west of False Bay. Figures for St. James are derived from Marchand 1932, for Muizenberg and Roman Rock from Isaac 1937.

The *P. cochlear* mosaic was sharply replaced at M.H.W.N. by *Bifurcaria brassicaeformis* in a luxuriant belt 0.25 metre broad. In it were a few other algae such as *Aeodes orbitosa*, *Gigartina stiriata* and *Ulva* spp., and there were many small *Mytilus perna*. From the upper limit of *Bifurcaria* to about M.H.W.S. the rock was dotted with a variety of algae in small numbers; the only ones that were not tiny were *Splachnidium rugosum* and *Gelidium pristoides*. Here, *Octomeris* was abundant but *Tetracrita* became more plentiful until at M.H.W.S. the latter dominated the rock at the expense of the former. Since the transect did not extend as high as E.H.W.S. the upper limit of *Tetracrita* could not be determined.

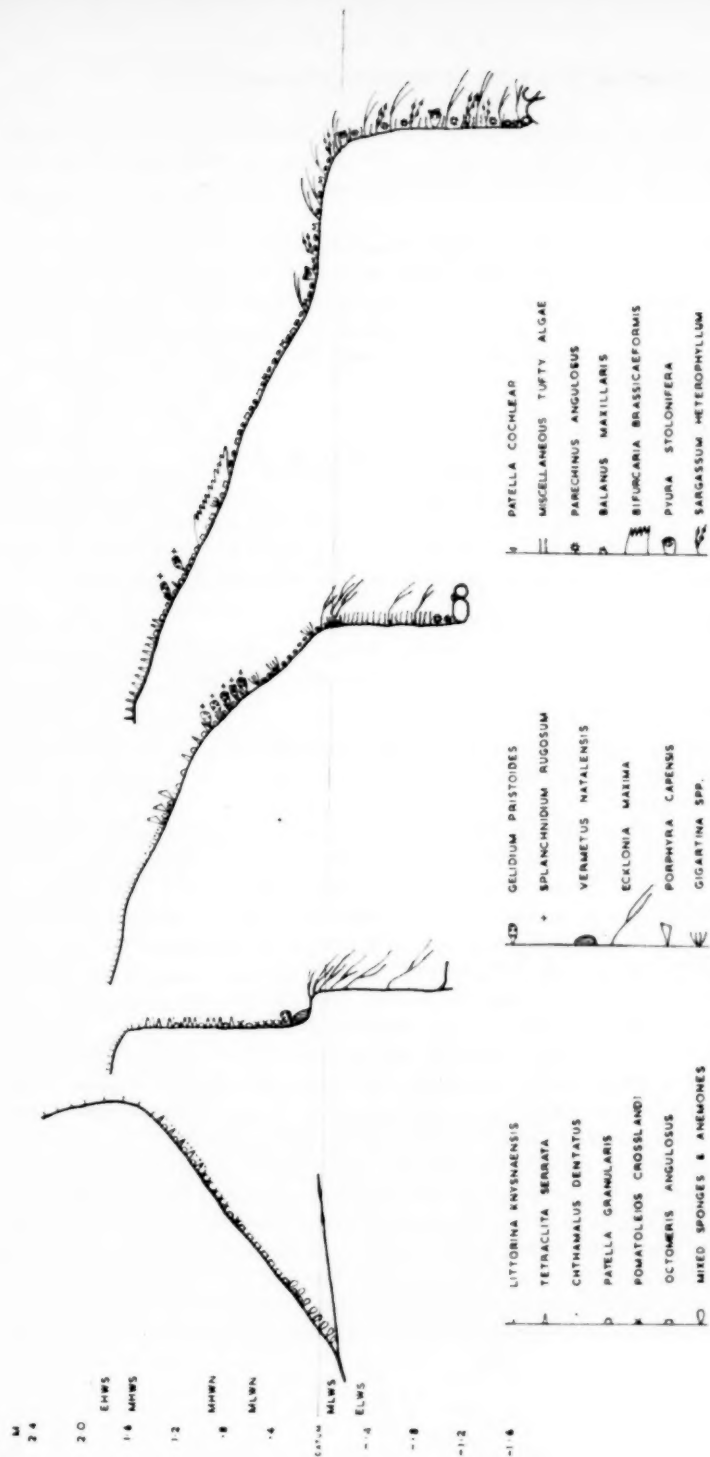


FIG. 4. Profiles of the intertidal transects with diagrammatic representation of the chief biota.
 From left to right the sites are: Shady, Very Sheltered; Semi-Exposed; Exposed. The vertical scales show true levels.
 To avoid confusion *Octomeris* has been omitted from the diagram of the Semi-Exposed site; its range and abundance are approximately that of *Gelidium*.
Pomatoleios crosslandi is a synonym of *P. knysii*.

The most important mobile species were *Patella granularis*, *Oxystele variegata* and *Burnupena cincta*, all with similar distributions throughout the *Bifurcaria* and barnacle zones, i.e. from M.H.W.N. to M.H.W.S. No *Littorina* was present at the crest of the transect.

The transect did not extend high enough to support a *Littorina* zone but surrounding rocks suggested the lower limit of this zone to be at E.H.W.S. level or higher. The Upper and Lower Balanoid zones merge just below M.H.W.S., at the upper limit of the assorted algae. The Cochlear zone has a sharp upper limit at M.H.W.N. and merges indistinctly with the top of the 'Sublittoral fringe' about 0.3 m. above M.L.W.S.

(v) *Comparative Distribution of the Chief Species*

A difficulty that arises in comparing the intertidal sites is that certain very characteristic but mobile species move about according to the state of the tide, sunshine, etc. It would be simpler to omit them from the following comparison but the decision is made difficult by the gradation from truly sessile to very mobile. Luckily it is unnecessary 'to split hairs' on this count and the following are omitted:

Amphineura: *Acanthochiton garnoti*.

Streptoneura: *Amblychilepus scutellum*, *Burnupena cincta*, *Littorina knysnaënsis*, *Oxystele sinensis*, *O. variegata*, *Patella granularis*, *Thais dubia*.

Asteroidea: *Asterina exigua*, *Henricia ornata*.

It will be noted that although *Patella granularis* is considered to be mobile, *P. cochlear* is regarded as a hemi-sessile species. This is justifiable because of the different habits of these two limpets.

The conspicuous sessile and hemi-sessile intertidal species of the sites are listed in Table IV in which their distribution is shown with an indication of their abundance. There is one proviso: species may be conspicuous at one site and present, but of negligible importance, at another. In the latter case they would be regarded in Table IV as absent: e.g. *Bunodosoma* was, in fact, present at Froggy Pond but only in small numbers and the individuals were tiny so that this anemone was not ecologically important there. A few algae have been omitted from the table because of difficulties of identification, e.g. *Ulva* spp. and jointed Corallines.

Table IV shows that the two exposed sites are far richer in variety of species than the sheltered ones. This cannot be certainly ascribed to differences in exposure since the two exposed sites are much flatter, and so greater in area, than the others. The Table illustrates the marked absence of important algae from the shady, very sheltered site, presumably due to the dim illumination.

It is interesting to test whether the species of the sites reflect differences in exposure. Only one species of the thirty-nine listed in Table IV has a discontinuous distribution in the series, this being the barnacle *Octomeris* which is present at the Shady, Very Sheltered site, absent from the Sheltered site, and present at the two Exposed sites. There is no obvious reason for this. The distribution of the other thirty-eight species is summarized in figure 5 which demonstrates a progressive change

	Shady, very sheltered	Sheltered	Semi- exposed	Exposed
<i>Algae</i>				
<i>Aeodes orbitosa</i>	—	—	FC	FC
<i>Bifurcaria brassicaeformis</i>	—	—	—	C
<i>Bifurcariopsis capensis</i>	—	—	FC	F
<i>Bryopsis</i> sp. (CP.413 F)	—	—	—	F
<i>Chaetangium ovale</i>	—	—	FC	—
<i>Chylocladia capensis</i>	—	—	FC	F
<i>Ecklonia maxima</i>	—	FC	FC	FC
? <i>Falkenbergia</i> sp. (CP.413 G)	—	—	—	FC
<i>Gelidium pristoides</i>	—	F	C	FC
<i>Gigartina radula</i>	—	—	C	—
<i>Gigartina stiriata</i>	—	—	C	F
? <i>Griffithsia</i> sp. (CP.413 H, CP.396 F)	—	—	C	FC
<i>Hypnea spicifera</i>	—	—	FC	FC
<i>Iridophycus capensis</i>	—	F	—	—
<i>Laurencia glomerata</i>	—	—	FC	—
'Cochlear Lithothamnion'	—	—	A	A
'Crusty Lithothamnion' (CP.392 B)	—	C	—	—
'Dusty Lithothamnion'	A	A	—	—
<i>Plocamium corallorhiza</i>	—	—	—	F
<i>Porphyra capensis</i>	—	—	C	—
<i>Pterosiphonia cloiophylla</i>	—	—	C	—
<i>Sargassum heterophyllum</i>	—	—	—	F
<i>Splachnidium rugosum</i>	—	—	C	C
<i>Porifera</i>				
? <i>Geodia littoralis</i> (CP.426 B)	C	—	—	—
? <i>Hymeniacedon perlevis</i> (CP.426 C)	C	—	—	—
<i>Polychaeta</i>				
<i>Menipea crispa</i>	C	F	—	—
<i>Actiniaria</i>				
<i>Bunodosoma capensis</i>	C	F	FC	—
<i>Polychaeta</i>				
<i>Pomatoleios kraussii</i>	A	A	F	—
<i>Streptoneura</i>				
<i>Patella cochlear</i>	—	—	C	C
<i>Vermetus corallinaceus</i>	—	A	—	—
<i>Pelecypoda</i>				
<i>Mytilus crenatus</i>	F	F	FC	C
<i>Mytilus perna</i>	—	—	FC	C
<i>Cirripedia</i>				
<i>Balanus maxillaris</i>	—	—	—	FC
<i>Balanus trigonus</i>	C	—	—	—
<i>Chthamalus dentatus</i>	C	FC	C	—
<i>Octomeris angulosus</i>	A	—	FC	A
<i>Tetraclita serrata</i>	A	A	A	A
<i>Tunicata</i>				
<i>Amaroucium ?erythraeum</i> (CP.428 B)	C	—	—	—
<i>Pyura stolonifera</i>	—	—	—	F
Total ..	12	12	23	22

TABLE IV

Distribution and relative abundance of certain sessile and hemi-sessile intertidal species.
 Symbols of relative abundance: A abundant. C common. FC fairly common. F few.

in species from the Shady, Very Sheltered site to the Exposed one with only two species, *Tetracita* and *Mytilus crenatus*, being common throughout. It seems clear that the gradation in exposure to wave action is accompanied by a gradual change in the commonest species present.

The vertical ranges of many of the commonest species are compared in figure 6. The top half of the figure shows those species present on three or four sites and the bottom half those present only on the Semi-exposed and Exposed sites. *Bifurcaria* is indicated as being present at the Semi-exposed site; actually it was not present in the transect but it formed a marked patch not 2 feet away on rock of similar slope and aspect. The widths of the diagrams are intended to give an idea of the relative abundance of each species. The top half of figure 6 shows a rise in the upper limits of all species save *Tetracita* from the Sheltered to the Exposed sites; and lower limits tend to a similar rise with the exception of *Oclomeris* and *Mytilus crenatus* (but the latter species is very common infratidally and the high position of its bottom limit at the Semi-exposed site is of local importance only). This tendency is usually not continued in the distributions of the same species at the Shady, Very Sheltered site where the added factor of shade is involved. The lower half of figure 6 shows very markedly that species always occur at high levels on the more exposed site. The average rise of the centres of distribution of the species of the two exposed sites is 0.47 metre when both the upper and lower halves of figure 6 are considered. A point to be noticed is that the actual vertical ranges of these species, and their relative abundance, often remains unaltered.

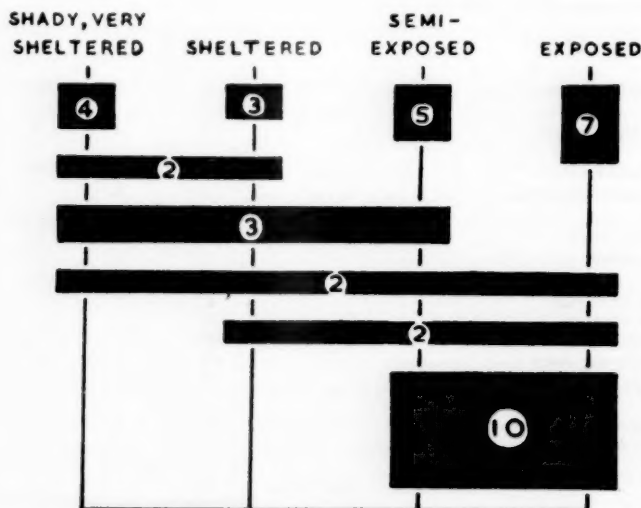


FIG. 5. The distribution of certain common sessile and hemi-sessile species between the intertidal sites.

The number of species in each group is given.

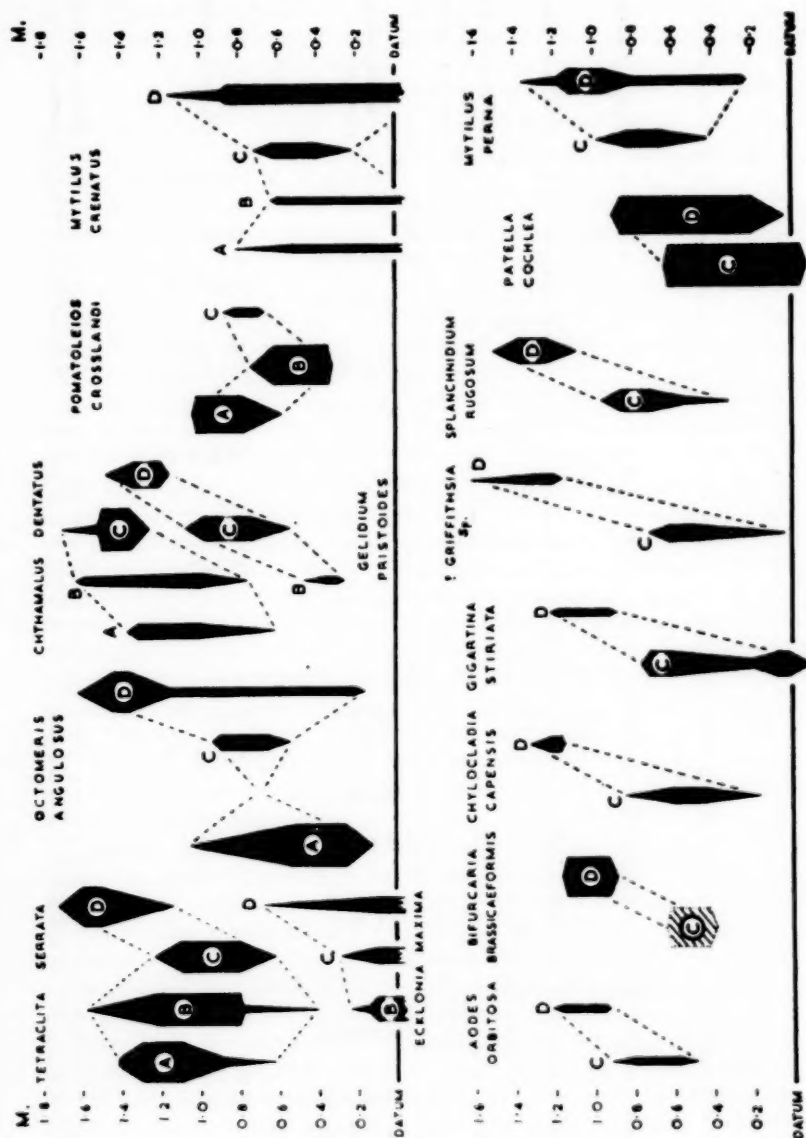


FIG. 6. Comparison of the vertical ranges and abundance of some common sessile species.

A: Shady, Very Sheltered site. B: Sheltered site. C: Semi-exposed site. D: Exposed site.
Bifurcaria is represented by hatching at the Semi-Exposed site because it was found just to one side of the actual transect.
 For '*Pomatoleius crosslandi*' read *P. kraussii*; for '*Aodes*' read *Aeodes*.

Height range (metres)	Number of lower limits	Number of upper limits	Total number of species	Difference between total number of species and total number of limits	True tidal positions (Simonstoun)	Effective tidal positions	Effective tidal levels (metres)
SHADY, VERY SHELTERED SITE. (13 spp.) Upwash 0.23 m. (9 in.)							
2.0-1.6	0	0	0	0	E.H.W.S.	M.H.W.S.	1.57
1.8-1.4	0	1	1	0	M.H.W.S.		1.37
1.6-1.2	0	2	2	0			1.17
1.4-1.0	0	5	6	1		M.H.W.N.	0.97
1.2-0.8	0	5	7	2	M.H.W.N.		0.77
1.0-0.6	2	2	8	4		M.L.W.N.	0.57
0.8-0.4	4	2	9	3	M.L.W.N.		0.37
0.6-0.2	2	5	11	4			0.17
0.4-0.0	2	4	9	3		M.L.W.S.	-0.03
0.2-0.0	2	0	9	7	M.L.W.S.	E.L.W.S.	-0.23
SHELTERED SITE. (12 spp.) Upwash 0.34 m. (1 ft. 1½ in.)							
1.8-1.4	0	2	2	0	M.H.W.S.		1.26
1.6-1.2	0	1	2	1			1.06
1.4-1.0	0	0	2	2		M.H.W.N.	0.86
1.2-0.8	0	0	2	2	M.H.W.N.		0.66
1.0-0.6	1	3	5	1		M.L.W.N.	0.46
0.8-0.4	1	5	7	1	M.L.W.N.		0.26
0.6-0.2	4	6	10	0			0.06
0.4-0.0	6	5	11	0		M.L.W.S.	-0.14
0.2-0.0	3	1	7	3	M.L.W.S.	E.L.W.S.	-0.34
0.0-0.0	1	0	4	3	E.L.W.S.		-0.54
-0.2-0.0	0	0	4	4			-0.74
-0.4-0.0	0	0	4	4			-0.94
SEMI-EXPOSED SITE. (26 spp.) Upwash 0.76 m. (2 ft. 6 in.)							
2.2-1.8	0	0	0	0			1.24
2.0-1.6	0	2	2	0	E.H.W.S.	M.H.W.N.	1.04
1.8-1.4	0	3	3	0	M.H.W.S.		0.84
1.6-1.2	2	2	4	0		M.L.W.N.	0.64
1.4-1.0	3	2	5	0			0.44
1.2-0.8	1	6	8	1	M.H.W.N.		0.24
1.0-0.6	1	14	16	1		M.L.W.S.	0.04
0.8-0.4	5	9	16	2	M.L.W.N.	E.L.W.S.	-0.16
0.6-0.2	7	3	18	8			-0.36
0.4-0.0	5	4	15	6			-0.56
0.2-0.0	7	4	15	4	M.L.W.S.		-0.76
0.0-0.0	5	3	13	5	E.L.W.S.		-0.96
-0.2-0.0	0	0	8	8			-1.16
-0.4-0.0	0	0	8	8			-1.36
EXPOSED SITE. (24 spp.) Upwash 1.26 m. (4 ft. 1½ in.)							
2.0-1.6	0	4	4	0	E.H.W.S.	M.L.W.N.	0.54
1.8-1.4	0	6	6	0	M.H.W.S.		0.34
1.6-1.2	0	6	10	4			0.14
1.4-1.0	6	7	13	0		M.L.W.S.	-0.06
1.2-0.8	10	7	18	1	M.H.W.N.	E.L.W.S.	-0.26
1.0-0.6	3	6	12	3			-0.46
0.8-0.4	0	5	13	8	M.L.W.N.		-0.66
0.6-0.2	1	4	13	8			-0.86
0.4-0.0	3	1	14	10			-1.06
0.2-0.0	6	1	13	6	M.L.W.S.		-1.26
0.0-0.0	4	0	11	7	E.L.W.S.		-1.46
-0.2-0.0	0	0	7	7			-1.66

TABLE V

Number of sessile species and their limits of distribution in relation to true and effective tidal levels.

The 'upwash' is the height by which true tidal levels are assumed to be raised to give effective levels.

The distribution of the conspicuous species may be further examined on the lines suggested by Colman (1933) to determine what levels are particularly critical. The foregoing descriptions have commented on the chief infratidal species at each site with this in mind so that the possibly critical region of the transition from intertidal to infratidal can be included in this analysis. In addition to the species of Table IV the following infratidally important species, all algae, are considered: *Caulerpa filiformis*, *Dictyota dichotoma*, *Dicurella fragilis*, *Dicurella flabellata*, *Leathesia difformis*.

Table V contains the results of analysis of the four intertidal sites (it corresponds to Colman's Table VII of p. 464). In smoothing his results Colman used intervals of 3 feet with overlaps of 1 foot, whereas here intervals of 0.4 metre (15.7 in.) are used with overlaps of 0.2 metre (7.8 in.). The data of Table V have been graphed against surveyed heights and analysis on the lines suggested by Colman shows that at each site certain levels are critical in regard to the upper and lower limits of distribution of species while other levels are not very critical.

The results, amplified by reference to distribution diagrams of the species of each site, are summarized in figure 7 from which certain inferences may be made. Firstly that the three well-illuminated sites show the following patterns from the Sheltered to the Exposed site. In all three the infratidal region below E.L.W.S., i.e. from -0.3 to about -0.7 metre, is not at all critical but from 0.1 metre below datum (M.L.W.S.) to 0.3 metre above it appears to be critical for the lower limits of most species of the lower intertidal zone. At the Semi-exposed site there is, in addition, the suggestion of a critical peak for the upper limits of infratidal species. Higher up, the pattern differs at each site with the critical levels extending higher where exposure to wave action is greater. Increasing exposure also separates the lower limits of species of the highest, middle and lowest intertidal zones, so much so that at the Exposed site a non-critical area appears between the latter two groups. Secondly, the pattern of critical levels at the Shady, Very Sheltered site is unlike that of the Sheltered site. In the shade the non-critical zone seems to extend above datum level (below -0.1 metre rock shape precludes comparison). Further comments will be made at the end of this section.

Colman suggested that tidal levels are effectively raised by wave splash and applied a correction of 2 feet for Church Reef, near Plymouth, England; and Bokenham, Neugebauer and Stephenson (1938) used a correction of 2.2 feet for four traverses in the St. James region of False Bay. Here, a different allowance must be made for each transect. These allowances have been termed 'upwash' and their calculation has been described above. They are given in Table V. It will be noted that the difference between the upwash of the two exposed sites is 0.50 metre, which is strikingly in agreement with the average rise in level (0.47 m.) of the centres of distribution of many species present at both localities (fig. 6 and p. 406).

If the height of any intertidal organism is considered relative to effective tidal levels its effective height is less than its height above datum by the upwash. The same pattern of critical levels is shown at each site but figure 8 shows that only at the Shady, Very Sheltered site do all the critical levels exist above effective datum.

Wave action moves the critical levels downwards relative to effective levels and spreads them apart vertically.

It is tempting to infer much more from figures 7 and 8 than has been said, but there are two very sound factors that make for caution. Firstly, this type of analysis treats dominant species exactly on a par with lesser ones. An example of the biased emphasis that may result would point the moral. Thus figure 7 shows that the critical level for the upper limits of species of the lowest intertidal zone is from 0.6 to 0.8 metre above datum. But the overwhelmingly dominant species of the lowest intertidal is *P. cochlear* and its upper limit occurs sharply at 0.62 metre. Secondly, the influence of shading and of exposure to wave action could only be neatly demonstrated by this type of analysis if the same species occurred on each site. But they do not and so the critical levels under discussion are not only affected by shade or exposure but by the different tolerances of different species to these factors and to one another. *P. cochlear*

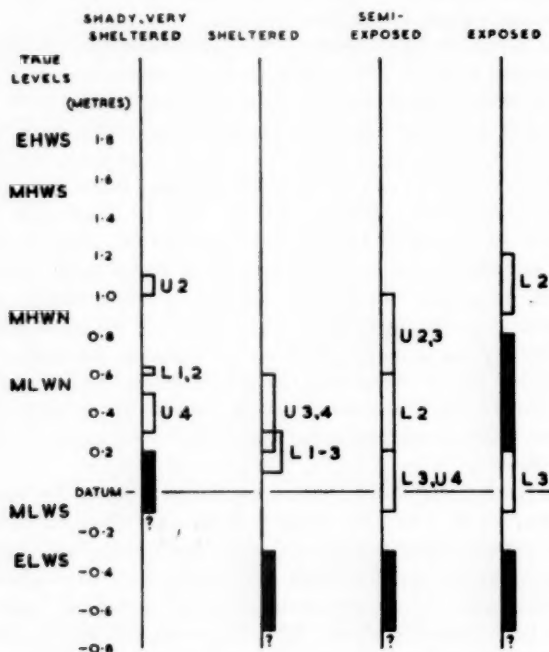


FIG. 7. Conspicuously critical levels (open boxes) and non-critical levels (black boxes) relative to datum and true tidal levels.

- U. Upper limits of distribution.
- L. Lower limits of distribution.
- 1. Species of highest intertidal levels.
- 2. Species of middle intertidal levels.
- 3. Species of lowest intertidal levels.
- 4. Species of the infratidal.

again provides the example for this is only found where wave action is more than moderate and when present it invariably dominates other species, moving their limits up or down as the case may be (fig. 4).

In summary, it may be said that although wave action raises most critical levels up a rock face (fig. 7), it lowers most of them relative to effective levels (fig. 8) and the former effect outweighs the latter because the biota actually occur higher with increasing exposure (fig. 6). Presumably, as argued by Colman, the raising of critical levels is due to wetting by splashing waves. The lowering relative to effective levels is a surprising finding and is not easy to account for save in generalities. Figure 8 shows that the lower limits of species of the mid-intertidal are to be found around effective E.L.W.S. and the upper limits of species of the lowest intertidal around effective M.L.W.S. But the lower limits of the lowest intertidal species move down markedly with increased wave action, and the upper limits of the infratidal species do the same. It seems that the species of the upper and middle intertidal regions maintain their critical levels relative to effective heights, according to expectation, but that the lowest intertidal species at exposed sites are more tolerant of effectively infratidal conditions and push their lower limits down at the expense of infratidal species. This is almost certainly due to exposed sites supporting species different from those of sheltered sites and not due to changed tolerances of species found on all sites.

Shading appears to raise the critical levels of intertidal species, whether relative to true or effective levels, but not to raise the upper limit of infratidal species.

To conclude this discussion on the intertidal sites, we may look at figure 4 with an eye to Stephenson's system of zonation. The upper limit of the Balanoid zone clearly rises with increased exposure and the division between Upper and Lower Balanoid zones follows this trend on the illuminated sites. The Cochlear zone raises the lower boundary of the Balanoid zone similarly but, with moderate wave action, it moves the 'Sublittoral fringe' downwards although this boundary also rises upon exposure being increased. This zonation shows, as it should, the same features as emerged above. Just as species move up a rock face with increasing exposure, so do the zonal boundaries; as some species are replaced by others with increasing exposure, altering the positions of the critical levels, so are the zonal boundaries modified.

Stephenson (1944) discusses the effects of wave action on these zones at some length in respect of the South Coast from Port Elizabeth to Cape Agulhas. Although False Bay is about 80 miles west of Cape Agulhas as the crow flies, Stephenson's remarks hold good. The Exposed site is probably not more than moderately exposed by Stephenson's standards due to its situation in a large bay (though it is fairly heavily exposed by European standards). The zonation at the Exposed site is that shown by Stephenson (1944) slightly to the exposed side of the centre of Plate XIII with modifications due to most of the species being at the westerly ends of their geographical ranges, e.g. *G. pristoides*, *Hypnea*, *Plocamium corallorhiza*, *M. perna*, *P. cochlear* and *Pomatoleios*. On the other hand, *Ecklonia* is present, although near its easterly limit, and *Bifurcaria* is a species that flourishes only in this region of overlap of the western and southern biotic components. The 'Sublittoral fringe' at the Exposed

site supports a mixed algal community, as is frequently the case, rather than a well-developed *Pyura* community, but the latter is common near by.

A. METHODS

INFRATIDAL BIOLOGY

The infratidal here was first explored with a diving hood by Mr. P. W. Jackson who very kindly lent me his apparatus. His work on the underwater ecology of Kalk Bay harbour is, unfortunately, unpublished. I found the diving hood to be too clumsy for regular use outside the protection of harbours and so replaced it with a self-contained, compressed-air diving apparatus of the 'aqualung' type which has been most satisfactory. Frogman flippers were preferred to weighted boots on the grounds of safety and mobility, and a waterproof suit was used when the water was cold. By force of circumstances, all diving was done alone, which has nothing to be said in its favour.

The usual equipment carried was: a sheath-knife at the belt, a scraping tool looped to one wrist and a collecting basket to which were attached a depth gauge and a writing tablet with pencil. Notes on these items follow.

Sheath knife. Useful generally. It should be heavy.

Scraping tool.

(a) 'Hand Hoe.' This consisted of the metal head of a garden hoe to the back of which was attached a pocket of coarse bolting-silk. Useful for scraping and then catching the floating debris. The heavier the instrument the better because underwater the swimmer can exert little leverage on his instrument. For this reason this tool was usually ineffective on limpets and large ascidians and algae.

(b) Abalone lever. A heavy tyre-lever with sharpened ends: used for the more strongly attached organisms.

Collecting basket. An item purchased ready-made. Made of galvanized-iron wire of interlocking spiral mesh which permitted collapse when empty. Mesh of about 1 cm. bar. Mouth circular, 13 cm. ($5\frac{1}{4}$ in.) diameter and closed by a spring-actuated flap opening inwards. The mouth was found to be rather small.

Depth gauges. Plastic manometer-type gauges supplied commercially for underwater sportsmen were found to give trouble. Excellent Bourdon-type pressure gauges are available but expensive. The gauge used was a car's Bourdon-type oil-pressure gauge of range 0-45 lb./sq. in. which was enclosed in a rigid, watertight, glass-fronted case. Through the case there led an extension of the Bourdon tube which opened to the sea through a filter of copper gauze. The filter had to be replaced occasionally since it clogged with salt, sand and debris. The gauge was calibrated in quiet water against a sounding-line, and occasionally checked. Readings appear to be accurate to 5 per cent.

Writing tablet. Talc sheeting affixed to either side of a painted board by drawing pins. Dimensions $12\frac{1}{2} \times 20$ cm. ($5 \times 7\frac{1}{2}$ in.). A red wax-pencil was used for writing. Not all wax-pencils are suitable. Wolff's 'Chinagraph' made by the Royal Sovereign Pencil Co., Ltd., has proved excellent. The pencil was sharpened at both ends and bound to prevent the wooden halves from separating. It was attached to the board by nylon line and a fishing swivel, and when not in use was secured by a rubber band. Board and pencil floated. Erasure was normally done by rubbing with finger or cloth but the talc was occasionally cleaned with carbon tetrachloride.

Underwater camera. A 35 mm., compur shutter Voigtlander 'Vitessa' camera was encased in a watertight aluminium box through which the following controls could be manipulated: focusing, wind-on and shutter tensioning, shutter release. The box was fitted with sports-type viewfinder and a manually operated exposure counter. Shutter speed and iris diameter had to remain constant once the case was closed but this was seldom found to be a drawback since electronic flash was usually employed. A 'Multiblitz' electronic flash outfit was used. The power unit of this was

carried in an aluminium box on the chest and the flash head was encased in aluminium and attached to the camera housing. A glass dome was specially made to cover the flash bulb and a special underwater reflector of stainless steel was designed and fitted externally. The electric cables ran loosely through 'Tygon' plastic tubing which joined the cases of the camera, power unit and flash head through garden-hose unions. The switch for the flash unit was transferred to a position in the camera box and was switched 'on' as the last action before fastening the camera case. The inside of the three cases and of the plastic tubing was pressurized by carbon dioxide contained in a 10 oz. capacity cylinder and admitted through a pressure-reduction valve actuated by external pressure so that the deeper the camera went the more high-pressure carbon dioxide was admitted. When maintaining any given depth supply of gas was cut off, and on ascending excess internal pressure was released by a blow-off valve. Adjustment of the two valves ensured that pressure in the camera case remained about 7 lb./sq. in. in excess of the surrounding water pressure and water never penetrated the apparatus. Misting of the lens and window never occurred due to the carbon dioxide quickly expelling the water vapour present in the enclosed air. The flash head and power unit were subject to this pressurization via the loose-fitting Tygon cables.

Use of the flash gave sharp pictures at the expense of natural lighting. Ilford H.P.3 film was used and experiment showed the underwater flash factor to be 70 with this equipment. The Meritol-Caustic two-bath method of development was used to gain contrast without loss of film speed but so far underwater results have always been rather soft. Exposures were usually made at f.8 over distances of 1.3-3 metres. In determining range, a half-metre stick was first attached to the face to be photographed; the size of the stick relative to the frame of the viewfinder enabled the range to be calculated. This photographic outfit produced excellent results in the clear water of the Mediterranean but in the comparatively dirty water of False Bay results have been disappointing. In dirty water, suspended particles scatter the flash beam just as mist scatters the headlamp beams of a car at night, and with the same confusion to the viewer. Without the flash, lighting is inadequate so that the vicious circle of adequate exposure, camera shake and depth of focus becomes unbreakable.

The method of examining a chosen rock or bottom was as follows. The site was reached by swimming if near to shore and by boat if far out. It was given a preliminary survey by aqualung and notes were made underwater; if sufficient air were left, some collections were made. As a result, certain areas were later worked in greater detail. To avoid confusion, the collecting basket was only used for material from one area at a time. Notes and collections were representative of the superficial biota but it was usually impossible to scrape away encrustations right down to the rock face and elements of this habitat would almost certainly be missed. Since the rock was of granite there was no infauna. Very active animals escaped capture but the largest (e.g. *Jasus*, *Plagusia*) could easily be noted. The Blennioid fishes and shrimps and prawns could not be identified or caught and so were disregarded. By putting many lumps of debris into the basket an astonishing variety and quantity of small animals were found on laboratory sorting (Amphipods, Isopods, Gastropods, Nematodes, etc.), but Turbellaria and Nudibranchs escaped from the basket during swimming.

In the shallows a short, buoyed 'sounding' line, or a bamboo stick of 1 metre length, was sometimes used to measure depth, but deeper readings were by depth gauge. Readings were later adjusted relative to datum of the Cape Town tide gauge.

B. THE BIOTA

(I) Oatland Point

Where the infratidal transects rose above low-tide level the chief intertidal biota were noted for the sake of completeness and to provide some biological indication of

the degree of exposure to wave action. These intertidal notes have not been discussed in the previous section because the levels were not surveyed.

Unfortunately, the intertidal biota did not indicate different exposure to wave action as 'typically' as one would like. Surprisingly, none of the sites possessed a mosaic of *Patella cochlear* which, if present at one or another, would probably be a useful guide. Nor was the biota arranged at any site in a pattern corresponding to one of the surveyed intertidal transects. This is lamentable but not surprising in view of the possible variations in the biota of apparently identical situations whereas these sites varied in aspect and slope quite apart from their exposure. However, some fair biological indications were given and they are interpreted below in the light of personal experience and of the remarks of Stephenson (1944). No attempt is made to compare differences in level of species or zones because intertidal levels were measured only very approximately.

(a) *The 'Inside' of Lagoon Rock*

The Lagoon side of Lagoon Rock (fig. 2) will be referred to as the 'inside' and the Channel side as the 'outside'.

The site faced SSW. and was not struck directly by the swell. It received further protection from adjacent rocks but, all the same, there were usually turbulent eddies across it due to the surf. The exposure was judged to be in the order of that at the Sheltered intertidal site, possibly rather more sheltered conditions were indicated biologically by the presence in the Lower Balanoid zone of abundant *Vermetus*, with '*Lithothamnion*', instead of a *P. cochlear* mosaic. The dominant barnacle was *Tetracita*, mussels were of negligible importance, and there was no *Pyura*, either in the infratidal fringe or infratidally.

The rock fell vertically from above the intertidal to the stony floor of the Lagoon at only 1 metre below datum.

The top of the infratidal fringe was at 0.3 metre above datum. It was well marked by the sharp upper limit of the kelp *Ecklonia maxima*; but the mossy-looking green *Caulerpa holmesiana*, and reddish *Gymnogongrus* sp. (FAL.308 D) were common on the rock and there were lesser numbers of *Dicurella flabellata* beneath the fronds. Since the site only achieved the depth of 1 metre, little can be said in the way of vertical zonation. All four algae extended to the bottom but the kelp flourished only in the fringe, decreasing sharply in both numbers and size at datum level, and *Gymnogongrus* did much the same. On the other hand *Caulerpa* increased as they decreased and it dominated the infratidal region.

The algae, particularly *Caulerpa*, obscured a mass of things, of which the largest were unidentified sponges, polyzoa (especially pink *Retepora* type) and compound ascidians such as *Distaplia capensis*, *Polyclinum arenosum* and two new species, *Amaroucium unilarviferum* and *Molgula falsensis*. These in turn sheltered feather-stars (*Comanthus wahlbergi*) and brittle-stars (*Ophiactis carnea* and *Ophiothrix triglochis*), and too many polychaetes to mention. The algae were heavily encrusted with the ascidian *Didemnum stilense* and small sponges (*Sykon* and *Leuconia*).

The algae showed considerable seasonal variation that was confusing. The inside of Lagoon Rock was further confusing in that the biota changed considerably

within a few yards in the horizontal direction. To the north there was a cave and the described biota gradually changed into cryptofauna of which characteristic outliers were small, pale orange sea fans (*Eunicella papillosa*, FAL.132 U). To the south the face received additional protection from swell from another rock and there were considerable differences in biota. The infratidal fringe and infratidal were

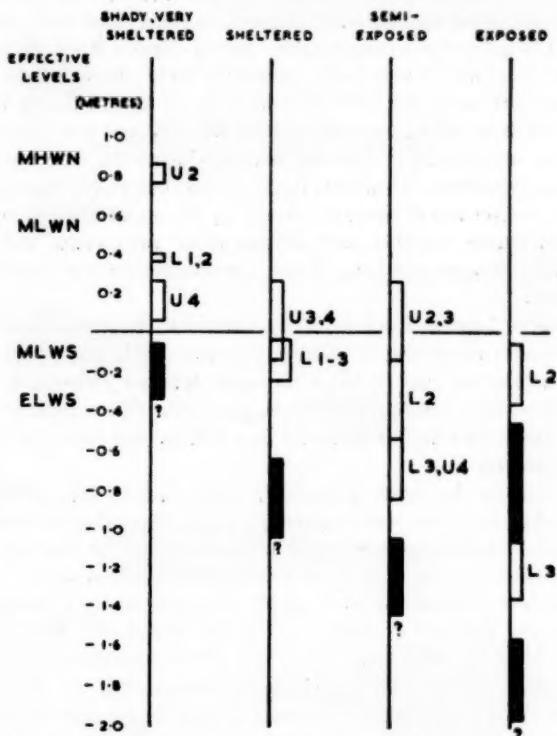


FIG. 8. Conspicuously critical and non-critical levels relative to effective tidal levels.

Allowance has been made for upwash at each site (as in Table V).
Symbols as in fig. 7.

dominated there by a '*Lithothamnion*' that permitted only a few small *Ecklonia* plants and which supported scanty epibiota, principally small anemones (*Corynactis annulata*) and a soft polyzoon (*Menipea crispa*). Whereas the described transect was like a thick, rich Persian carpet, this very sheltered part of the rock was like a polished stone floor. Its sanitary-looking bareness was relieved by groups of brightly coloured sea urchins (*Parechinus angulosus*), and, indeed, such arrangements of urchins on '*Lithothamnion*' were characteristic of many shallow rocks in the Lagoon.

(b) *The 'Outside' of Lagoon Rock*

The rock faced NNE, which made a slight angle away from the prevailing swell so that exposure to wave action was greater at the south-eastern end than at the north-western, but the change was gradual. The south-eastern end is chiefly considered here and its exposure was considered to be of the same order as that of the Exposed intertidal site, although the nature of the wave action differed at the two places. At the intertidal site the swell changed to rollers and surf just off the rocks and the impact of the surf was considerable. But at Lagoon Rock the swell remained unchanged and there was no true surf to pound the rocks; however, shearing currents of bubbly water tore across the rock faces with the rising and falling water.

Among biological indications of exposure we may first note the absence of the Cochlear mosaic and conclude that this may be due to the different nature of the exposure, as just remarked. However, the level that one might have expected to be occupied by *P. cochlear* was dominated instead by the alga *Bifurcaria brassicaeformis*, a lover of bubbly water, together with *Mytilus perna* *M. crenatus* and the barnacle *Octomeris angulosus* in large numbers. These corroborate the comment that exposure was considerable.

The outside of Lagoon Rock fell almost vertically from above the intertidal to the Channel bottom which was at about 5.3 metres depth here. The only break in the drop was a diagonal step or ledge no more than 0.8 metre wide (the biota of which are omitted from consideration). In plan view the straight part of the face was about 10 metres long and broken only by a narrow cleft from top to bottom near the north-western end.

The situation on the more exposed, or south-eastern, half of the face was as follows. The infratidal fringe rose to about 0.3 metre above datum where were found the upper limits of such important, shallow-water species as the kelp *Ecklonia*, the ascidian *Pyura stolonifera*, the tufted algae *Plocamium corallorhiza* and *P. cornutum*. The rock was dominated infratidally by a carpet of mixed algae, a patchwork of reds, browns and greens that hid a profusion of small animal life. Although *Pyura* was fairly common here the animal was small and either solitary or in little colonies of three or four; it tailed off before reaching the bottom (fig. 9). *Ecklonia* was more abundant than *Pyura* but although it formed a thick fringe around the rock—like a monk's fringe of hair below his tonsure—the plants became tiny and scanty below 2 metres depth. In fact, the chief colonizer of the top 2 metres was the feathery, red *P. corallorhiza* which, half-way down the infratidal face, was invaded by fair quantities of the brown algae *Dictyota dichotoma* and *Sargassum heterophyllum*. Further down, all these were replaced by the red *Dicorella flabellata* and green *Caulerpa holmesiana*. The lowest metre of rock supported, as was often the case, a community typical of the adjacent stony bottom. Here, the rock appeared very bare, except for scattered sea-urchins (*Parechinus*) and large anemones (*Pseudactinia flagellifera*), but actually was covered with 'Lithothamnion' and there were many tiny anemones (*Corynactis annulata*) and barnacles (*Balanus* spp.) upon it.

The north-western end of the face was less exposed, as has been mentioned, and intertidally this was reflected by an absence of *Bifurcaria*, decrease in the abundance

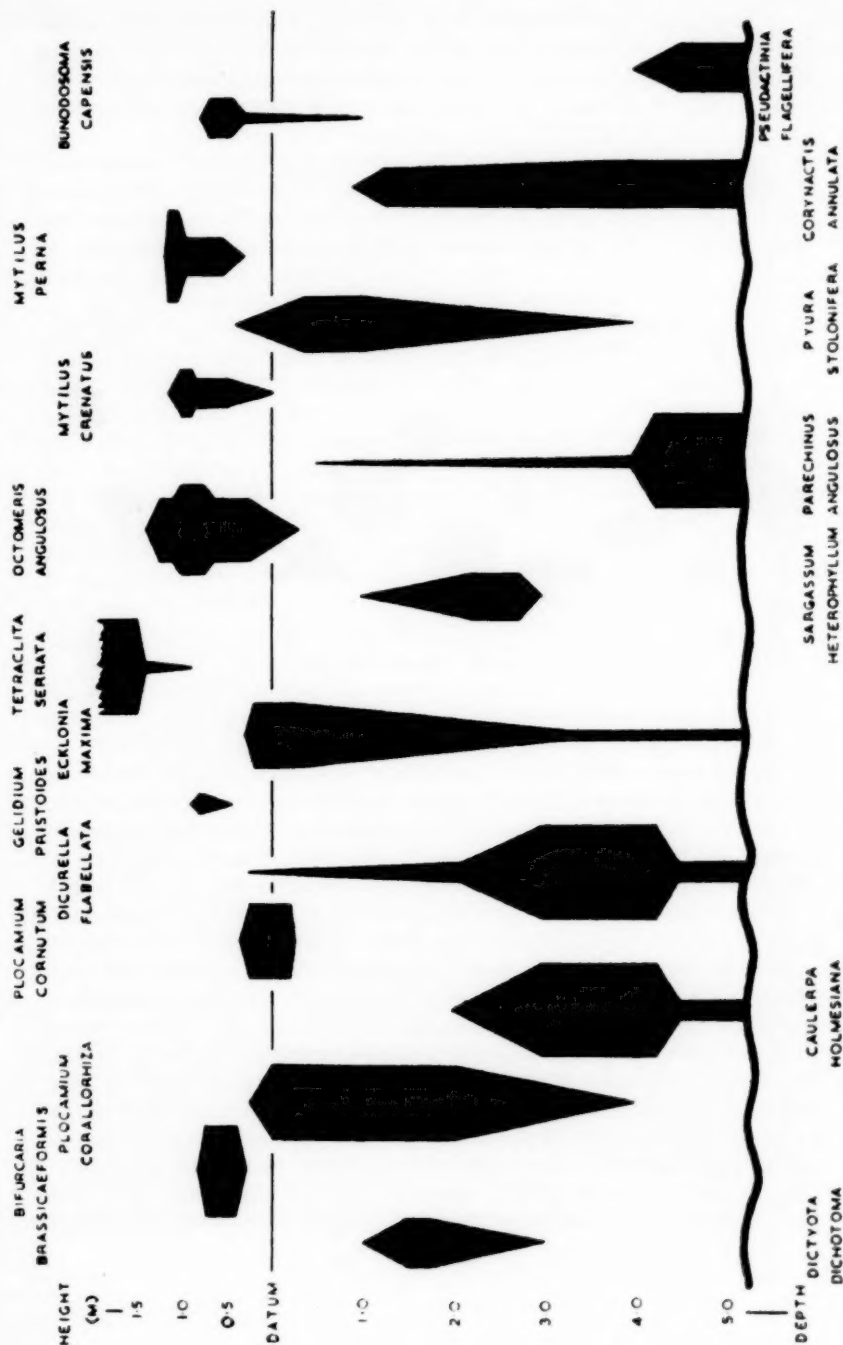


FIG. 9. The 'outside' of Lagoon Rock, at the more exposed end: diagram of the vertical distribution and abundance of conspicuous species.

of mussels and descent in level of *Tetracrita* (fig. 10). It seemed that the upper 2 metres or so of the infratidal also reflected this change of exposure. Here *Ecklonia* and *Pyura* were more luxuriant and especially so in the shelter of the vertical cleft. But the main difference was that *P. corallorhiza* was rather ousted by *D. flabellata* which dominated the algal carpet from E.L.W.S. almost to the bottom.

This site was examined in March 1953 and checked in April 1955 and the pattern was similar on both occasions. Detailed differences were the abundance of fluffy reddish and greenish epiphytes (such as *Falkenbergia rufolanosa*) on the first date and their scarcity on the second; and the replacement of much *C. holmesiana* by *C. bartoniae* on the latter date.

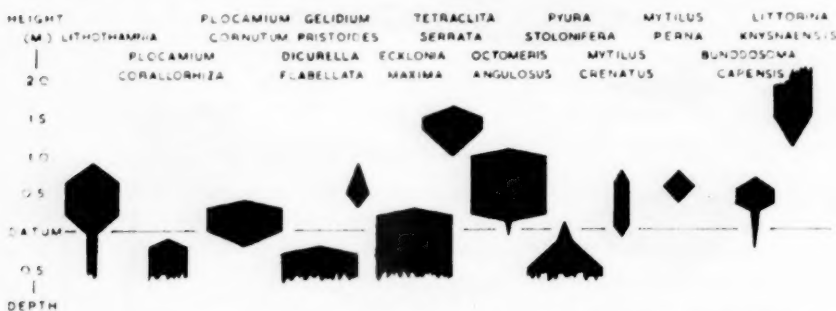


FIG. 10. The 'outside' of Lagoon Rock, at the more sheltered end: diagram of the vertical distribution and abundance of conspicuous species around datum level.

(c) The Channel Side of Big Rock

In plan view this had a bulge (fig. 2), the south-eastern part facing SSW, and the north-western part facing WSW. Swell ran very obliquely on to the former face and almost along the latter which was, therefore, a trifle less exposed. The exposure of both parts was judged to be a trifle more than that of the south-eastern part of the outside of Lagoon Rock. *Tetracrita* was absent from the south-eastern part here, and only present in a narrow band on the north-western (fig. 11); this barnacle does not thrive in very exposed situations. The Lower Balanoid zone of the whole face was dominated by a dense growth of *Octomeris* on *Mytilus perna*, suggesting that exposure was submaximal. *P. cochlear* was absent although abundant just around the corner from the face considered, to the north-west of Big Rock, where there was shelter.

The length of Big Rock is about 30 metres but the ends have split from the main body and are separated by vertical clefts. The centre section, which is the part that was examined, is unbroken. The rock fell vertically without pause from well above the intertidal to the bottom at 6 metres depth. Because of this, and its aspect, the biota were almost perpetually in the shade.

Before describing the biota, two convenient phrases must be established regarding the size and abundance of the giant ascidian *Pyura stolonifera*. This was usually found in alternative growth forms although there was, of course, intergradation. The one

will be called 'Pyura community': this applies when the tests are full-sized and closely packed. Then *Pyura* is the overwhelmingly dominant species of the rock. The phrase, loosely applied, includes many species that are commonly associated with *Pyura* in this growth form (cf. usage of Eyre, 1939, who lists some of the subordinate associated species). The other is 'Scattered *Pyura*' which refers to scattered, usually small individuals in clumps of a dozen or so; in this form, *Pyura* is a subordinate member of a community dominated by other species and the ascidian is accompanied by very few of the species characteristic of its 'community' form.

The more exposed, or south-eastern, part of the rock will be described first and then differences in the direction of greater shelter will be noted.

Spring tides always exposed a fringe of *Ecklonia* which was rather luxuriant and large down to E.L.W.S. but rapidly diminished in size and importance lower down. This fringe of kelp occupied rather precisely the extent of the infratidal fringe. As at Lagoon Rock, across the Channel, *Plocamium corallorhiza* was common among the holdfasts but here it was subordinate in importance to a dense sheet of mussels, overgrown by barnacles, that extended downwards from the intertidal (fig. 11). It was by no means easy to discern the limits of the various species but the one largest in size was *Mytilus perna* which was abundant at the top of the fringe but scarcely penetrated below it, so far as could be seen. It became increasingly invaded by medium-sized *M. crenatus* below M.L.W.N. level and this was the dominant species of the rock face down to about 2 metres depth. Intertidally *M. perna* was covered by *Octomeris* but from the infratidal fringe downwards the important barnacle was *Balanus algicola* which covered the mussels in such abundance as almost to obscure them.

It has been mentioned that *Ecklonia* became insignificant below the infratidal fringe and that the other species usually so important in this habitat, *Pyura*, was only found here in its 'scattered' form half-way down the face of the rock.

The general impression of the infratidal biota was of a great variety of rather small species, particularly algae, polyzoa, hydroids, anemones and ascidians, but, unfortunately, most of the algae seemed to show seasonal fluctuations. *Zonaria ?interrupta* (FAL.309 A) might have been the most constant for it was a major constituent of the biota all over the rock both in May 1953 and April 1955. On the former date *Sargassum heterophyllum* and *Caulerpa holmesiana* were of importance over the ranges shown in figure 11, but both were inconspicuous in April 1955 and instead *Plocamium ?membranaceum* (FAL.153 J) and a fine red algal fluff of the *Falkenbergia* type were common. Soft, tufty polyzoa such as *Bugula dentata*, *Menipea crispa*, *M. triseriata* and *Onchoporella bombycina* abounded here and were commoner than rigid polyzoa. Most hybrids were small but were very abundant, especially *Aglaophenia pluma* v. *parvula*, *Kirchenpaueria pinnata*, *Sertularella arbuscula* and *Plumularia setacea*. The most conspicuous anemones were the two large species, *Bunodosoma capensis*, at upper levels, and *Pseudactinia flagellifera*, lower down, and there were many bright green clusters of the small *Anthothoe stimpsoni*; the little pink *Corynactis annulata* was ubiquitous. Eleven species of ascidian were found here apart from scattered *Pyura*. The commonest was undoubtedly the encrusting *Didemnum stilense* and, next to this, *Amaroucium erythraeum*; other common species were *Distaplia capensis*, *Botryllus magnicoecus*, *Clavelina*

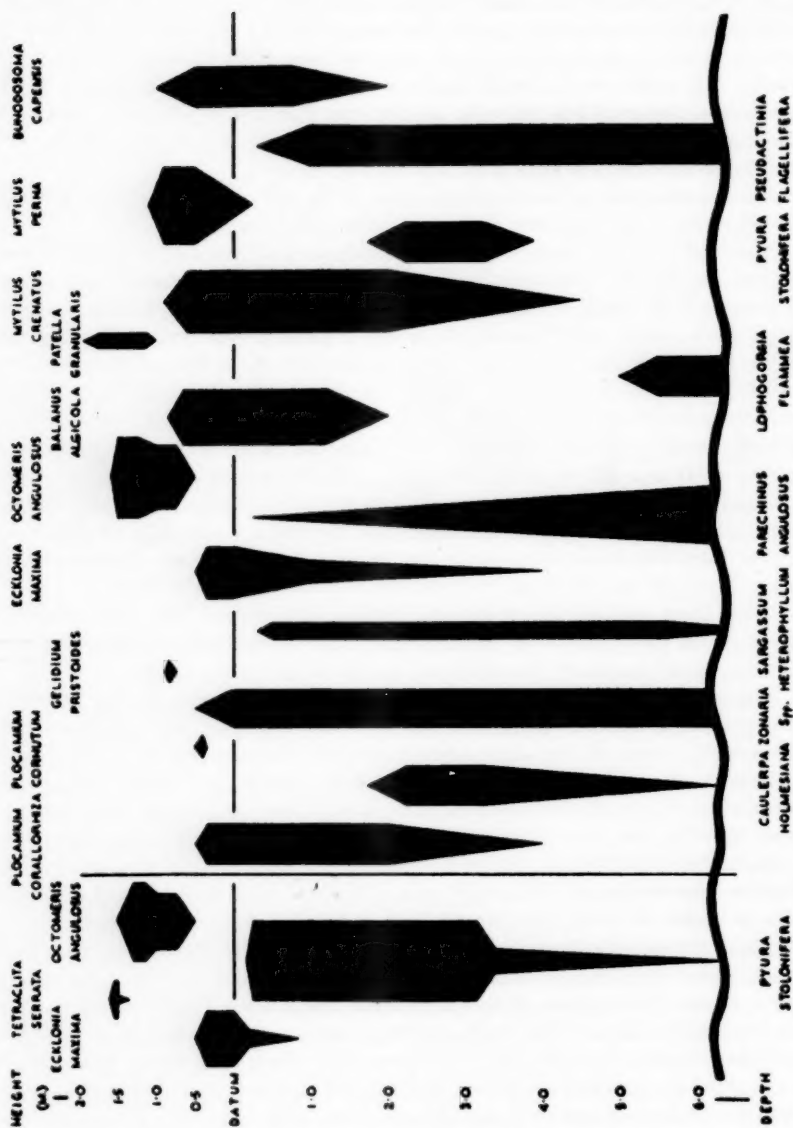


FIG. 11. The Channel side of Big Rock: diagram of the vertical distribution and abundance of conspicuous species. To the left of the diagram the main differences to be found at the north-western end are indicated.

steenbrasensis and *Pseudodistoma africanum*. The barnacles *B. trigonus* and *B. maxillaris* appeared to be common and fairly common respectively at any depth but they were scattered and inconspicuous. Two very conspicuous animals that were characteristic of the face were *Parechinus*, scattered almost everywhere and the great scarlet sea-fans *Lophogorgia flammaea* that occurred no shallower than 5 metres depth although typical of the rock below this. Attached to and crawling among these species was a multitude of polychaetes, small crustacea and small echinoderms.

On the slightly less exposed face to the north-west there were very striking differences in the shallowest 3 metres of rock but scarcely any below that depth. Everything depended on the fact that there *Pyura* flourished in 'community' form from E.L.W.S. downwards which ousted the mussels, the barnacles and *P. corallorhiza* and restricted *Ecklonia* to the infratidal fringe. The *Pyura* community did not quite cover all the rock but great, wedge-shaped stands of it reached down to about 3 metres. Where the *Pyura* community was absent scattered *Pyura* was often to be found especially from 2 to 3.5 metres depth.

The *Pyura* community provided a great increase in area available for colonization and the tests were in fact heavily, although not completely, covered. In the top metre 'Lithothamnium' and short, corallines such as *Arthrocardia* sp. (FAL.176 B) were the commonest epibiotas and deeper down there were many locally dense populations of *Anthothoe stimpsoni*, various hydroids (e.g. *Aglaophenia pluma* v. *parvula*, *Kirchenpaueria pinnata* and *Sertularella fusiformis*) and barnacles (*B. algicola* and *B. trigonus*). *M. perna*, *M. crenatus* and *Didemnum stilense* were really quite common although the mussels were tiny. Difficulty in removing the tests made examination of the hidden species difficult but *Bunodosoma*, *Pseudactinia*, *Parechinus*, *Marthasterias glacialis* and *Burnupena papyracea* were much in evidence.

(d) *Shallow Cave* (fig. 2)

A fairly extensive cave was found beneath Lagoon Rock. It really consisted of the gaps between several adjacent rocks and its irregular, ramifying crevices were too narrow to permit much penetration by a diver. The essential features of the accessible parts of this complicated cave appeared to be as follows. There was a reasonable amount of indirect illumination and the several openings, distributed at various depths, permitted fairly strong currents through it. Most of the bottom of the cave was at about 2½ metres depth and consisted of clean, coarse, shelly sand. In one place the top of the cave opened on to the northern end of a face already considered, the 'inside' of Lagoon Rock.

Four groups of animals dominated the biota—sponges, polyzoa, ascidians and hydroids—and it is most unfortunate that identification of the first two groups has been so fragmentary. It is impossible to comment adequately on the many species of sponges and polyzoa but the lack of comment must not convey an underestimate of their importance in the cryptofauna. Some common soft polyzoa that were identified were *Onchoporella bombycina*, *Menipea ornata*, *M. crista* and *Bugula robusta*; the pretty hard, pink *Retepora* near *tessellata* (FAL.154 L) was also common. The ascidians were similar in size to the sponges and polyzoa. There was a thick carpet of the sandy-

looking *Amaroucium retiforme*. On a horizontal ledge at about E.L.W.S. level *Pseudodistoma africanum*, *Distaplia capensis* and two new species of *Molgula* (FAL.158 Q, R) were common; but *Pyura* was virtually absent, being found only at high levels in the entrance. Although hydroids were extremely numerous and varied (some twenty species were found) they were usually epizootic in nature excepting *Sertularella arbuscula* (particularly common underneath rocks) and *Halecium beanii*.

Algae were definitely unimportant but several were to be found in small numbers in the best-lit places. Near the surface, for example, were sparsely distributed small red algae, chiefly *Dicurella* spp. and *Plocanium* spp., and a little jointed coralline, *?Jania* sp. (FAL.153 E), while at the lower entrances to the cave *Caulerpa holmesiana* was quite common. *Ecklonia* was virtually absent.

Some species of other taxonomical groups managed to be abundant among the profusion already indicated. For example, the crinoid *Comanthus wahlbergi*, which, like *Sertularella arbuscula*, particularly favoured the undersides of ledges, and the anemones *Pseudactinia* and *Corynactis*, were everywhere although the former only grew large near the sandy bottom. The little sea-fan *Eunicella* sp. (FAL.154 G) was a characteristic species of the cryptofauna although it was not really abundant. Three tubiculous polychaetes formed locally dense populations, viz. *Phyllochaetopterus socialis*, *Filograna implexa forma salmacina* and *Potamilla reniformis*. There were also many small polychaetes, small molluscs, isopods, amphipods, and three species of *Balanus*. Two brittle-stars were commonly found beneath the rich growth of fauna, namely *Ophiactis carnea* and *Ophiothrix triglochis*.

Some idea can be gained of the great variety of life here from the relatively few species mentioned above. No area of rock was free of a rich, thick growth of fauna, and the conspicuous species hid a profusion of smaller ones and bore numerous epizoa. Over one hundred and fifty species were listed from the small confines of this cave despite its shallow depth range. The irregular ramifications of the cave did not lend themselves to exhibiting vertical zonation of the biota but, except for the sparse algae, no such zonation was noticed. Unfortunately, it was not possible to follow changes correlated with progressively decreasing illumination, for dark corners were inaccessible.

The cave was inhabited by many fish, especially *Diplodus sargus*, *D. trifasciatus*, *Coracinus capensis*, *Gymnocrotaphus curvidens* and *Palunolepis brachydactylus*, but most of these have been driven away by the activities of spear-fishermen. Similarly the ranks of crawfish, *Jaes lalandii*, have been sadly thinned by man, probably far more so than by the occasional octopus (*Polypus granulatus*) that has been observed to chase them.

(e) *The Lagoon Bottom*

The topography of the Lagoon is shown in figure 2 from which it can be seen that the main openings in its periphery are at the south and the north. Since the prevailing swell is from the south-east the Lagoon is well protected, particularly at low tide when many shallow peripheral rocks become exposed. The southern opening itself received considerable protection from a group of rocks to seaward, but if a

heavy swell is running, waves have time to reform and to enter the opening obliquely. Surf frequently spills into the Lagoon over the south-eastern rocks and small waves come in through the northern opening, but large waves seldom pass across the Lagoon. Due to the direction of the prevalent swell there is often a weak current of water entering the southern opening and a stronger one going out of the northern, but much depends on conditions of tide and wind.

The landward margin of the Lagoon consists of granite blocks and slopes with many rounded, sandstone boulders piled up intertidally and in the shallows. The large rocks of the Lagoon are of granite; the bottom consists chiefly of rounded sandstone boulders and stone with gravel and some patches of coarse, shelly sand. The distribution of these deposits correlates with that of water movements, for the sand is almost confined to the south-east where it is deposited from the dying surf. Most of the bottom lies at about 1 to 2 metres depth, the deepest places being over the sandy patches.

The following observations were made of the rocks and stones of the Lagoon bottom, avoiding deep cracks between them. The biota was extremely characteristic due to the domination of '*Lithothamnium*' which covered over three-quarters of the available rock. There appeared to be two main types: a thick, pink one that was lobed at the edges (FAL.182 D) and a filmy-thin, lilac-coloured type (FAL.182 C). The former seemed to be commoner on vertical faces down to 1 metre and probably was identical with the one (CP.392 B) at the bottom of the Sheltered intertidal site (p. 398). Many of the shallow rocks had bare-looking, slimy areas of a red-brown coloration that suggested the presence of a coating of *Myxomycetes*. Encrustations of brown algae of the *Ralfsia* type were common and the remaining rock surface was colonized by various tufted algae, limpets and anemones. Epibiota were very sparse on the '*Lithothamnium*', on the slimy brown patches and on the ?*Ralfsia*, and so the bottom looked very bare because of the great area that these algae covered.

In regard to sessile species, especially the tufted algae, it was difficult to determine whether they grew upon the '*Lithothamnium*' or were primary colonizers of the rock. Jointed corallines such as *Amphiroa* spp. and *Arthrocardia* spp. were quite common, and soft algae such as *Aeodes orbitosa*, *Dictyota dichotoma*, *Bifurcariopsis capensis*, *Sargassum heterophyllum* and *Zonaria interrupta*. *Ecklonia* was limited to the immediate vicinity of large, upstanding rocks, growing at their bases and on their vertical faces. Limpets were very common, namely *Patella miniata* and *P. barbara*, which, with *P. tabularis*, were found in the ratio of 14:9:2 (in a count of twenty-five random specimens). Identification of these was impossible without dislodging them because the shells were heavily epiphytized with jointed corallines or, less commonly, with tiny algae such as *Chylocardia capensis*, *Champnia compressa*, *Leathesia difformis*, etc. A whole host of small animals such as polychaetes (*Platynereis dumerilii* was particularly common) molluscs and ophiuroids found shelter impartially among these epiphytes and in similar ones on the rocks. The anemones *Pseudactinia* and *Anthothoe* were fairly conspicuous although not very abundant. They favoured vertical faces, especially near the bottom.

There were various mobile species found on the rocks and, particularly, in the

shallow crevices between them. *Parechinus* and the little gastropod *Oxystele sinensis* were especially characteristic. Other common ones were the gastropods *Turbo sarmaticus*, *T. cidaris*, *Burnupena papyracea* and *Argobuccinum argus* and the starfishes *Henricia ornata*, *Patiria granifera* and *Asterina exigua*.

Although the sandstone and granite seemed to be impervious to infauna, the thick, lobed '*Lithothamnion*' was penetrated by many polychaetes and it enveloped several species such as the little bivalve *Saxicava arctica*. It was very often not actually attached to the rock but separated from it over areas of at least several square decimetres, and this sheltered, gloomy space contained a rich cryptofauna of polyzoa, polychaeta, pelecypoda, amphipoda and ascidians. The shells of the patellids and of *Turbo sarmaticus* were bored by the polychaete, *Polydora capensis*.

It remains to mention two very characteristic species of the bottom which were not conspicuous to the eye. Hidden beneath the jumbled stones there were clusters of the elegant, black brittle star *Ophioderma leonis*; and, half-buried in little pockets of sand among the stones, there were many blackish holothurians, *Cucumaria stephensoni*.

(f) *The Channel Bottom*

The Channel separated the seaward group of rocks at Oatland Point from the landward by 25 metres or more (fig. 2). It lay in line with the prevailing swell which became progressively reduced towards the north-west because the Channel widened there. Diving was done in a moderate swell which was found to produce no strong motion at the bottom, at 5-6½ metres below datum.

The bottom varied in nature. About half of it, chiefly to the north-west, was of clean, shelly sand and the rest consisted of stones and rocks around a pronounced but discontinuous median reef. It was difficult to make a hard and fast distinction between the 'typical' bottom and the rocks jutting up from it, but collecting was confined to stones and low rocks and avoided larger rocks and the reef. Overhangs and dark crevices were also avoided so that notes should refer only to typical, open, flat-bottom biota.

The chief impression of the rocks was that they were colonized by small patches of various algae. '*Lithothamnion*' was common (FAL.147 Z) but it was the tufty algae that were conspicuous, chiefly the browns, *Sargassum heterophyllum* and *Dictyota dichotoma*, and the red *Aeodes orbitosa*. Green patches of *Caulerpa holmesiana* and *C. filiformis* were quite common and, where present, completely dominated the biota thereabouts. Other green algae were *Codium duthieae* and *C. stevensiae* which were common enough but never dominant species. Reddish algae of the *Gymnogongrus* type were fairly common, and the fine, woolly *Falkenbergia rufolanosa* formed a thick, pinkish, epiphytic fluff in places. Various other algae were present in lesser degree, including jointed corallines of which the commonest was *Arthrocardia attenuata* (FAL.147 V). *Ecklonia* was virtually absent since it was only represented by tiny juveniles.

Animals were inconspicuous among all these algae. The commonest sessile species included many coelenterates, viz. the anemones *Pseudactinia*, *Anthothoe* and *Corynactis*, the hydroid *Plumularia setacea*, *Alcyonium ?fallax* (FAL.148 F) and the

scarlet sea-fan *Lophogorgia flammea* which did not grow large here. Three barnacles were common, *Balanus albigula*, *B. trigonus* and *B. maxillaris*, of which the first two were dominant in places but never the last.

Many hemi-sessile species were to be found among the stones and in small crevices. The most conspicuous was *Parechinus* but many gastropods were scarcely less so, e.g. the large *Turbo sarmaticus*, *Argobuccinum argus* and *Burnupena papyracea*; and also *Cucumaria insolens* and *Ophiothrix triglochis*. As in the Lagoon, *Ophioderma leonis* gathered under stones and *Cucumaria stephensoni* in sandy pockets. The only large, very mobile animals were the crawfish *Jasus lalandii* and the octopus *Polypus granulatus*.

(II) Noah's Ark

A brief visit was made to this interesting rock and a collection was made from a small part of its vertical northern face from 11 metres down to the bottom at 14 metres.

This part of the face was completely colonized by a rather monotonous short growth lacking large or flamboyant species. Surprisingly, the little pink anemone *Corynactis* was almost of greatest importance for here it was larger in size than at Oatland Point. (It also lacked its typical white margin.) These anemones were partly hidden by a lot of the hydroid *Aglaophenia pluma* v. *parvula* among which small *Mytilus crenatus* were common but, of course, well hidden. There were occasional, large *Pseudactinia*. Many lumps of large, derelict *Balanus maxillaris* shells suggested that this barnacle had once been plentiful. Colourful large starfishes, *Marthasteria glacialis*, roamed all over the rock.

(III) Roman Rock Lighthouse

Several visits were paid to this locality in an attempt to find the deepest rocks, and the collections and notes were made of three areas. Since the biota of these areas was by no means similar each will be described separately. As in the foregoing accounts, only the large and important species will be mentioned.

(a) 35 metres WNW. of Lighthouse

The vertical, sloping and horizontal surfaces of a group of low rocks at 12 to 14 metres depth were examined but dark crevices and overhangs were avoided. There was no obvious difference in the biota to be correlated with the angle or aspect of the faces.

The most distinctive feature of the area was a dense 'doormat' of small *Mytilus crenatus* anchored upon old, dead *Balanus* shells. Upon this mat short hydroids were common, in particular *Aglaophenia pluma* v. *parvula*. Where the mat was absent hydroids of many species were widespread, other common ones being *Nemertesia cymodocea*, *Sertularella arbuscula* and *Antenella africana*. Some were heavily epiphytized by a red, very finely branching alga (*Ceramium* sp. FAL.278 B). In general, algae were not rare but they were inconspicuous: *Dicurella* ?*flabellata* (FAL.274 B), *Plocamium* ?*membranaceum* (FAL.268 A) and *Gigartina* sp. (FAL.278 D, E) were to be seen if searched for, and also little jointed corallines. Patches of *Anthothoe* and *Corynactis* were common and other coelenterates were *Lophogorgia* and orange ?*Gorgonia*

albicans (FAL.279 A). A beige sponge (FAL.274 X) was conspicuous and there was one patch of the tubes of *Phyllochaetopterus socialis* covering about half a square metre in which there were numerous isopods (e.g. *Exosphaeroma planum* and *Cirolana sulcata*) and tiny gastropods. Two huge oysters, *Ostrea atherstonei*, were a pleasant discovery. Large, hard polyzoa of the *Chapperia* type were present but uncommon. Three notable absentees were *Ecklonia*, *Pyura* and *Pseudactinia*. Several mobile species were common, particularly the starfishes *Marthasterias* and *Henricia*, the two cucumbers *Cucumaria insolens* and *?Pentacta* sp. (FAL.272 B), and *Argobuccinum argus*.

(b) 90 metres ESE. of Lighthouse

Observations and collections were made of the sloping surfaces of huge, rounded granite rocks between 12 and 17 metres depth. The almost vertical and almost horizontal surfaces had much the same biota but overhangs and dark crevices were avoided.

The primary coating of the rock seemed to be dead *Balanus* shells, certainly in many places, but no sheets of living *Balanus* were to be found. A mat of small *Mytilus crenatus* commonly grew on this, as occurred at the site, just described, 35 metres WNW. of the lighthouse. Although several square metres of rock might be dominated by the mussel, it was so sand-sprinkled as to be inconspicuous. The other biota presented a very 'tussocky' appearance because of many gorgonians such as *Lophogorgia* and *?Gorgonia albicans* (FAL.268 S), and because of big alcyonacea such as the brown, cauliflower-like *?Capsella rugosa* (FAL.268 U) and *?Heteroxenia capensis* (FAL.268 V). Further examination added to the impression of abundant coelenterates for there were colourful anemones of several sorts everywhere (including the ubiquitous species, *Corynactis* and *Pseudactinia*) and many hydroids were common, e.g. *Nemertesia cymodocea*, *Sertularella arbuscula* and *Salacia articulata* (of which the first two were usually epizootic on the sea-fans). Cup-corals of the *Balanophyllia* type were also quite common.

The above coelenterates comprised the chief sessile species; the hemi-sessile and mobile species were drawn from another group, the echinoderms. Several were very common such as *Marthasterias*, small in size, and crinoids—the orangy arms of *Tropiometra carinata* and *Annametra occidentalis* flared from the rock in great clusters. Cock-robin holothurians, *Cucumaria insolens*, and purple ones, *?Pentacta* (FAL.272 B), were as numerous but more hidden. Several *Astrocladus euryale* were seen, two of them climbing a *Lophogorgia*, and the additional presence of occasional starfishes, *Patiria granifera* and small *Parechinus*, suggested that the echinoderms were almost as important as the coelenterates. The gastropod *Argobuccinum argus* was also very common here.

Throughout this depth range there were no tendencies to vertical zonation but it is interesting to record that the deepest patches of *Pyura* community hereabouts were at 12 metres. There was an absence of such typical fringe species as *Ecklonia* and the gastropods *Turbo sarmaticus*, *Oxystele sinensis* and *Haliotis midae*. The rarity of algae should be emphasized for only one small, red species, *Plocamium ?membranaceum* (FAL.268 A), was found and it was very sparse.

(c) 75 metres SE. of Lighthouse

A rock face fell vertically from about 8 metres to 15 metres depth at which it rested on a sloping rock that disappeared beneath shelly sand at 17 metres.

At 14-15 metres the chief colonizer was *Balanus trigonus*, with *Corynactis* almost as common. Other important features were big, beige, encrusting sponges (FAL.274 X), a purple *Chapieria*-type polyzoon, and great bunches of hydroids, principally *Sertularella arbuscula* and *Nemertesia cymodocea* with epizootic species. Gorgonians and alcyonaceans were present, but not in large numbers; *Pseudactinia* was common and vermilion *Balanophyllia*-type corals fairly common. There were a few crinoids, all of which seemed to be orange *Comanthus wahlbergi*, and three species of starfish, viz. *Marthasterias*, *Henricia* and *Patiria*. There were no holothurians and no mat of *Mytilus crenatus* although occasional, small specimens were present. *Argobuccinum* was common. In regard to algae, there were only sparse *Plocamium ?membranaceum* and sparse *Dicurella ?flabellata* (FAL.274 B).

It was interesting to find *Pyura* in community form at the top of the rock face, i.e. at about 8 metres, below which occasional, scattered *Pyura* extended as deep as 14 metres.

(IV) The Quay, Gordon's Bay Harbour

The vertical face of the quay consisted of rough-faced stone blocks with deep, narrow crevices between them. The face was examined from 0 to 3 metres depth.

The quay, in conjunction with the rest of the upper end of this little harbour, was very sheltered and all the biota, rocks and harbour fittings were coated in fine silt for tidal currents here were very gentle. In March 1953, the most conspicuous feature was a growth of fine, fluffy, reddish and greenish algae (FAL.137 T, U) which covered almost everything, including living sea-fans. It has not been possible to check this face at another season to determine whether these algae were seasonal such as the fluffy *Falkenbergia* that was abundant outside Lagoon Rock, at Oatland Point, during the same month.

The biota looked very drab because of the fluff and the silt. Even the scarlet *Lophogorgia flammea*, which was common though small, did little to brighten up the masonry. Fanworms such as *Sabellastarte longa* and the polychaete *Andouinia australis* found homes between the blocks and their protruding tentacles looked less dusty than anything else. The only other sessile species were the tunicates *Styela costata* and a *Pyura*-type species (FAL.137 N); the former often supported little barnacles, *Balanus trigonus*, and the hydroid *Plumularia setacea*. On the other hand, quite a few mobile species were seen, from the largish crab *Plagusia chabrus* to small polychaetes and amphipods. *Parechinus* was rather common, as was the big starfish *Marthasterias*, and there were a few gastropods such as *Clavatula sinuata*, *Burnupena cincta*, *Argobuccinum argus* and *Aplysia juliana*.

(V) Comparison of the Infratidal Sites

The infratidal sites may be grouped according to environmental conditions to determine whether generalizations are possible. These generalizations can only be

made regarding the localities visited and will certainly require modification for places in the north and in the south of False Bay, if only because of the changed abundance of *Ecklonia*.

(a) *Shallow, Vertical Faces*

Oatland Point, Inside and Outside Lagoon Rock, and the Channel Side of Big Rock. Depth range 0–6 metres.

Two facts are outstanding: that the rock surface is completely colonized and that there is a very great variety of species. Except where *Pyura* community takes over the rock or, less commonly, where *Mytilus* does so, the biota is dominated by algae, particularly by tufty, non-corallines. The common species are not banded into zones, as occurs intertidally, but it is clear that vertical gradients in distribution exist, even within this small depth range. Such gradients are shown in two ways: by changed abundance of individual species with depth, e.g. *Ecklonia*, which is most abundant around datum level and becomes scarcer deeper down; and by species actually occupying different levels in succession, e.g. *M. crenatus* in and below the infratidal fringe, and *Lophogorgia* only deeper than 5 metres.

The biota also change in a horizontal direction where the exposure to wave action changes. Again the abundance of individual species is affected and their presence—or absence. For example, a sheltered face may be colonized by *Caulerpa holmesiana*; a rather exposed one by *Plocamium corallorhiza* in upper levels and by *C. holmesiana* lower down; a more exposed one by *Pyura* in the shallows and *C. holmesiana* lower down; and one with submaximal exposure by *Mytilus* in the shallows and *C. holmesiana* lower down. This illustrates the fact that shallow levels are more affected by exposure than deeper and, in fact, one can go further and venture to say that below 2 metres depth the biota scarcely reacts to different degrees of exposure.

This is the most appropriate place to emphasize that the appearance of infratidal rocks in False Bay depends largely on two species, both giants of that habitat in size and importance, namely *Ecklonia* and *Pyura*. At Oatland Point *Ecklonia* is in conditions representing the end of its geographical range and consequently it is restricted in abundance and reacts sensitively to environmental pressures. It thrives where there is shelter and a lot of bubbly water: for instance, in crevices to leeward of rocks around which the swell breaks. But where exposure is great it is, surprisingly, most abundant around datum level: it appears to require the well-aerated water there more than it shuns the turbulence, but this is probably an over-simple deduction. In addition, the abundance of *Ecklonia* depends greatly on that of *Pyura*. *Pyura* is in almost optimal climatic conditions, and where there is strong exposure and a lot of 'soda water' it usually ousts *Ecklonia* and everything else except its special friends and hangers-on. These comments only apply to the region around Oatland Point. Further south, near Cape Point and across the bay near Cape Hangklip, *Ecklonia* competes with *Pyura* on at least equal terms down to 3 metres and has no rival below that to about 10 metres depth.

(b) *Shallow, Vertical Face in Sheltered Water*

Gordon's Bay quay. Depth range 0–3 metres.

By no means all the rock is colonized, unless by microscopical algae, and there is no great variety of species. The rock and biota are covered by silt and look very drab. There are no tufted algae, and, apart from epiphytes, the sessile species are all animals, e.g. hydroids, sea-fans, fanworms, barnacles and ascidians which do not show zonation. Such a combination of species was not found elsewhere.

This type of site is not known well enough for further generalization, and the one examined, at Gordon's Bay, is too far from the other stations for elaborate comparison since hydrological differences probably confuse those due only to shelter. Time did not permit the completion of work that was planned for other harbours.

(c) *Shallow Cave*

Oatland Point, beneath Lagoon Rock. Depth range 0-2½ metres. Plenty of indirect light.

The rock is completely colonized and a great variety of species is present in profuse abundance. Certain groups of animals are characteristic and dominate the biota between them, namely the porifera, polyzoa, coelenterata and ascidiacea. Distribution is patchy and does not show vertical zonation. Algae are absent from the cave proper and *Pyura* is also absent doubtless because of the low illumination and lack of very turbulent water respectively.

(d) *Shallow Rocky Bottoms*

Oatland Point, the Lagoon and Channel Bottoms. Depth range 1-6½ metres.

The rock seems to be completely colonized except where it lies next to sand which commonly scours all life from a basal strip of a few inches height. The biota appears to change rather sharply at about 3 metres depth.

Down to 3 metres the rocks and stones are dominated by bare-looking expanses of '*Lithothamnium*' and, to a much lesser degree, by *Ralfsia*-type encrusting algae and probably by *Myxomycetes*. On these rocks epibiota are very rare in comparison with rocks free of these algal encrustations. They consist of tufted algae (including many jointed corallines) and limpets in about equal proportions, but the limpet shells provide further substratum for algae. Because of the bare appearance of the bottom the mobile animals, sea-urchins, gastropods and starfishes, strike the eye more than elsewhere and the combination of colours is very pretty. In the crevices between the large rocks there is plenty of kelp but it does not grow on the open stony bottom. There is no *Pyura*.

Stony bottoms at 4-6 metres lack the abundance of encrusting algal forms and support instead rich patches of tufted, soft algae, all of which also occur sporadically in the shallows. However, *Ecklonia* is virtually absent (except in the south of False Bay) and other conspicuous absentees are the limpets and *Pyura*.

(e) *Moderately Deep Rocks*

Noah's Ark; Roman Rock at three sites. Depth range 11-17 metres.

The rock is completely colonized and there are very many different species. There are two dominant groups, coelenterates and echinoderms, but the commonest

species of these are not the same as those that are typically found in a shallow cave. Hydroids, alcyonaceans, gorgonians, holothurians and asteroids are particularly common. Distribution is patchy and there is no vertical zonation or gradient; neither does it depend upon the slope of the rock, nor its aspect. A feature of these faces appears to be the presence of mats of small *Mytilus crenatus*. The mussels are usually attached to abundant dead *Balanus* shells although sheets of living *Balanus* are rare. Algae, including *Ecklonia*, are virtually absent and there is no *Pyura*.

Several interesting points result from comparing the above groups. Except for the very sheltered site which is very silty, all infratidal rocks are completely colonized, without a square centimetre remaining bare (unless scoured by sand). It is striking that a great variety of species colonize the rock except where silt acts as a drastic presence-or-absence factor or where '*Lithothamnion*' occupies a great deal of space, as on very shallow rocky bottoms.

The abundant or dominant species of one group are usually not abundant in another, or even present at all. This merely proves what is to be expected: that different species flourish under different conditions. In general, algae dominate well-illuminated rocks down to 7 metres, but plants give way to animals between 7 and 10 metres. Below this depth algae are virtually absent. Naturally enough, algae are excluded from caves, however shallow.

One can say that there is no sharp vertical zonation comparable to that in the intertidal zone yet it is quite clear that the biota changes with depth even within the small range considered here. For instance, the biota at 2 metres bears little resemblance to that at 6 metres and none to that at 12 metres (although, of course, certain species occur throughout). It has been mentioned that the biota of the shallowest metre or so varies tremendously according to exposure: in other words, it varies horizontally around a rock. But this tendency rapidly ceases with increasing depth: even at 2 metres the influence of exposure on the biota is markedly less pronounced and at 6 metres it is hard to discern. The influence of slope also decreases with depth for in the shallows the biota of vertical faces differs from that of horizontal faces while at 12 metres there is no difference.

CONCLUSIONS

It is now possible to compare the arrangement of life on intertidal rocks and on rocks below tidal levels at one locality. It appears that the work that was done is certainly useful, but perhaps inevitably it shows that much more must be done to dot the i's and cross the t's of our interpretation of the influences at work.

The most useful conclusions drawn from this work are given below but no attempt is made to discuss exhaustively all environmental influences on an animal because the general principles are well appreciated today (e.g. see Gislen, 1929 and 1930).

A. THE EFFECTS OF EMERGENCE

Undoubtedly the most important distinction between the intertidal and infratidal zones is that the former is periodically exposed to air. In False Bay the chief

hazards of a marine creature that is left bare by the water are desiccation and overheating, and only species that can withstand these conditions can survive. Thus emergence exerts a drastic selective effect on species in the intertidal and does not affect infratidal species at all.

Different levels of the intertidal become exposed to the air, or 'emerge', for different periods of time. Bokenham *et al.* (1938) have calculated the percentage emergence at Simonstown, a mile or two north of Oatland Point, and have obtained a sigmoid curve that is shown in their text-figure 8 relative to tidal levels. The curve shows that the rate of change is greatest at about the levels of M.H.W.S. and M.L.W.S. and fairly constant throughout the central metre of the intertidal, on either side of M.S.L. Thus, descending a sheltered rock, marine conditions become important rather suddenly at about M.H.W.S. level, increasingly important at a steady rate lower down, throughout the middle of the intertidal zone, and then, suddenly, more important still at about M.L.W.S. level below which emergence virtually ceases. Because of the great rate of change around M.L.W.S. it is interesting to compare the percentage emergence at our datum (not that of Bokenham *et al.* which is about 10 inches lower down) with that at M.L.W.S., the figures being about 3 per cent and $\frac{1}{2}$ per cent respectively (personal communication from Dr. N. A. H. Millard, née Bokenham).

Apart from desiccation and heating, which are by far the most important aspects of emergence, there is another aspect that may be important in regard to wave action. When steep rocks are left uncovered by the tide algae hang under the influence of gravity but submerged plants are almost unaffected, or even buoyant.

The importance of emergence is shown by the fact that where it is great, as at the top of the intertidal zone, much of the rock is bare and only a few species are to be found. On the other hand, the lowest intertidal rocks are 100 per cent colonized and support a great variety of life. Clearly, the sharp zonation of the intertidal region is due to the effects of emergence acting over so small a vertical range. There is no infratidal environmental feature of comparable importance.

Emergence may be effectively decreased at any level by the upwash of waves, especially on exposed rocks. This will be discussed later. It is likely that tufted algae effectively reduce the emergence of small species in their shelter so that they are found at higher levels than on open rock, but this work has not provided conclusive evidence.

B. THE EFFECTS OF LIGHT

The decrease in illumination as one passes underwater is surprisingly small: the shallowest metre or two is almost as well illuminated at noon as the intertidal zone. Earlier and later in the day more light is reflected from the surface and less passes through it. Although there is no sudden decrease in illumination at the surface it is true that the intertidal is fully lit while the infratidal never is, a progressive and differential absorption occurring with every metre's depth. There is no local work on light absorption in sea water but Grein's work (1913) in the Mediterranean may be comparable if one remembers that False Bay water never approaches the clarity of the water in which he worked.

Sudden drops in illumination—far greater than that at the water's surface—are found both intertidally and in the shallows due to shading. This may be due to rock formation or to a canopy of algae, e.g. *Ecklonia*. Even in the open air shading may be enough to suppress the presence of algae, as was found at the Shady, Very Sheltered intertidal site; and underwater the effect is pronounced as was shown by the shallow cave where algae were absent.

It seems likely that the levels where the greatest changes in the biota occur, the critical levels, are also affected by shade for they appeared to be higher on the shaded intertidal site. Since algae were unimportant there, this raising of critical levels must be due to decreased heating and decreased desiccation.

The loss of light with depth is accompanied by a decrease in algae. Thus, algal distribution on well-lighted, intertidal rocks is not governed by illumination, for there is ample light, but below about 10 metres depth lack of light enables animals to compete successfully for space.

It is tempting, but unwise, to attempt to explain the different biota of shallow flat, sloping and vertical rocks in terms of illumination. Detailed work is necessary to do this and other factors such as exposure to turbulence and sedimentation are likely to be more important.

C. THE EFFECTS OF TURBULENCE

Of the many aspects of turbulence the one that is chiefly regarded here is the direct, mechanical effect of water movement on biota. This, too, has many aspects, for it can be fast or slow, have various horizontal and vertical directions, be constant, variable or oscillatory and if it changes in nature it can change quickly or slowly. The phrase 'wave action' has been used to cover this sort of turbulence in the intertidal zone. The whole of the intertidal zone is exposed to wave action but infratidal water movements are much less violent and are different in nature.

Wave action is effective above and below the water's surface and different levels of the intertidal rocks are subjected to wave action in turn as tides rise and fall. Naturally, a rock is more often pounded between neap-tide levels than between those of spring tides; the amount of wave action to which any level is subjected is not related to the emergence curve. The effect of the crest of the wave is exaggerated when surf flows up a rock because of its momentum and the effect of the trough is always minimized because of cascading water. This matter has been raised earlier in calculating the extent of the upwash and suck-back of waves breaking on the intertidal. The suck-back of a wave hides from view the fact that cascading water descends well below the surface, certainly for 2 metres or more when the swell is fairly strong.

Colman (1933), among others, has remarked that wave action effectively raises tidal levels so far as living organisms are concerned. Certainly, this work has shown that the centres of distribution of many species rise where exposure is greater (fig. 6); and there is a remarkable correlation between the height of this rise and the roughly calculated estimate of wave upwash (see p. 309). As the intertidal work has shown, increased exposure affects the height and arrangement of the critical levels as well as those of the actual species. Increased exposure spreads the critical levels apart and

it raises them relative to surveyed heights (or predicted tidal levels). In the middle and upper intertidal regions the critical levels stay at about the same effective tidal levels but the lowest intertidal species spread relatively lower, into what is effectively the infratidal, and appear to push down correspondingly the top limits of infratidal species. This is probably due to the descent of cascading water into the infratidal and is probably a result of its turbulence, or velocity, acting directly (rather than via other effects, e.g. aeration).

It is clear from a glance at a broken coastline that increased wave action at exposed places has caused certain species to flourish there while others flourish in sheltered places. In other words, turbulence affects the presence or absence and the abundance of species, as has been clearly shown by the intertidal work here. Since False Bay has a swell that always comes from the south the exposure of a rock depends largely upon its aspect and so different sides of a rock support different species at the same level. Turbulence, therefore, cuts across the picture of vertical zonation and causes horizontal differentiation, or patchiness.

Infratidally there is no turbulence of the same magnitude as is found intertidally although cascading water descends violently for 2 or 3 metres below a rock face when a strong swell runs. Other infratidal currents are gentle in comparison and negligible in this context, and turbulence consists of oscillatory movements as the waves pass overhead. In other words, the water does not rush around but rocks gently to and fro. The difference between rushing and rocking water is the difference between surf and uncrested swell. The frogman knows well that the former will throw him on to a reef and drag him across it. But, even in a fair swell, he can lie a few inches off a vertical rock and will only be lightly tapped against it—the impact is cushioned, presumably by reflection of the swell from the rock. Surely the different natures of these forms of turbulence affect the species on the rock? There is also the effect of gravity to consider. Above water level it not only adds to the force of pounding waves and to the rush of cascading water, but algae have to contend with their own weight suddenly as waves withdraw. Below the surface the effect of gravity on plants is nullified.

The infratidal biota follows these changes in turbulence closely. It has been shown that where exposure to wave action is considerable the dominant forms of the lower intertidal region extend downwards for a metre or two below datum (fig. 11) which corresponds with the depth to which cascading water descends. Beneath this depth, about 2 metres, turbulence suddenly becomes low and it decreases rapidly and steadily with further depth. Under conditions of moderate swell algae were found to stream quite strongly at 6 metres depth but there were no very obvious correlations of distribution with aspect to suggest that turbulence influenced them. At 12 metres the rocking of the water was very gentle and appeared to have absolutely no effect on the distribution of the fauna. The horizontal patchiness of species due to varying strength of wave action thus disappears with depth but it is recalled that deep rocks still showed patchiness, which could not be attributed to wave action or illumination or to any obvious environmental feature.

Two other aspects of turbulence need mention. In the shallows, rocks that lie next to sand are often abraded by it around their bases. This only occurs where there

is strong turbulence; it is a frequent sight on rocks that lie next to a beach, where water is constantly sloshing about and carrying sand with it, but it is not a feature of even very shallow bottoms where surf is absent.

Where turbulence is very low silt is deposited from dirty water. This occurred at one of the examined sites, the quay at Gordon's Bay harbour, and quite obviously the silt had a great effect on the biota there, decreasing its abundance and eliminating many species. These effects were seen in the shallows; none of the deeper diving-sites showed silt so presumably the currents over them were too strong to permit it to settle.

D. DISCUSSION

Many of the differences between the intertidal and infratidal environments can be given point by the following story.

A frogman looks at the swell. It is only moderate but, with a fresh southeaster blowing behind it, there are lines of surf marching on to the beaches. He would take a lot of buffeting if he swam through those breakers. So he goes along a rocky point and finds at the end of it that the rock drops steeply to a nice depth, 4 or 5 metres. Although the end of the point is more 'exposed' than the rocks in the bay, next to the beach, and although the swell there rises and falls alarmingly, the frogman prefers that hazard to the force of the tumbling surf. He watches the swells carefully, to avoid being bowled over, and launches himself when a smooth crest laps his feet. He thinks how pleasantly cool the water is in contrast to the rock and as the suck-back takes him away he kicks hard to get beyond the reach of the next crest. A dive, and he is below the swell, looking for fish in the dim crannies, while the water's surface clouds over with soda-water cascading down from the following wave. The frogman, a comparative stranger to the sea, reacts directly to many of the environmental features of the intertidal and infratidal zones, heat, light, exposure, etc. He also knows perfectly well that the intertidal and infratidal biota appear very different and that the species overlap.

The main effects of emergence, light and turbulence have been considered above and, in general, their changes have been matched by changes in the biota. This does not quite complete the picture and so it is worth while finally to look at changes that occur in the biota and attempt to explain them in terms of the environment.

In South Africa the intertidal zone, proper, is very narrow—only 1.66 metres (5.44 ft.) between the mean high and low levels of spring tides—but the vertical zonation is very conspicuous. Quite obviously this is a result of emergence. The highest sessile species, the barnacles, are found only below M.H.W.S. on a sheltered rock and this is the height at which submergence becomes suddenly important. The other sharp boundaries in the intertidal—those between Upper/Lower Balanoid and Lower Balanoid/Cochlear zones—are not easy to account for precisely, but presumably are the result of balance between emergence and inter-specific competition.

As Stephenson has noted there is a striking change in the biota at the lowest levels of the intertidal zone, viz. in the infratidal fringe. Stephenson (1939, p. 512 etc.) does not define the upper limit of the fringe except rather vaguely in terms of

biota because the upper limit varies in level as well as in constituent species. In this paper the fringe is more sharply defined (p. 395) as the part of the infratidal region (i.e. below our datum) that is exposed by unusually low spring tides (E.L.W.S.). Figure 4 shows how the upper boundary, biologically, fluctuates around datum but is usually above it. This can be readily explained. Emergence decreases suddenly around datum level and becomes negligible below it, and this clearly is the cause of the biological change. The analysis of critical levels corroborates the importance of the upper boundary of the fringe for the most consistently critical level was around datum. It is interesting that although the lower boundary of the fringe is not clearly defined biologically its presence is suggested by the fact that the most consistently uncritical level occurred from E.L.W.S. downwards.

Clearly, the species of the infratidal fringe are infratidal in nature since they are only present where emergence is negligible. As there is no sharp lower limit to the infratidal fringe on a scale comparable to the intertidal zonation we may say that the fringe is not a zone in itself and that its upper boundary is the biological boundary between the inter- and infratidal regions. Actually, the fringe is dominated by species (e.g. algae, *Pyura*) that quickly diminish deeper down. After more extensive infratidal work it may be possible to differentiate a zone called the infratidal fringe. Certainly, its vertical range would be much greater than that of the whole intertidal zone.

Before leaving the intertidal region comment must be made on the effect of wave action on the biotic levels. This work has shown how species are moved up a rock by the upwash of waves, a well-known phenomenon. It has also been shown that where exposure is very great the dominant, lowest intertidal species extend very much lower to dominate the fringe and the topmost metre or two of the infratidal (fig. 11). These species do not entirely supplant typical fringe species, such as *Ecklonia*, and their upper limits are higher than those of the typical fringe species. Their upper limit is determined by emergence but their downward extension corresponds very markedly with the influence of cascading water. Certainly these species, mussels and barnacles, oust most others where the water pours in torrents; and so, where exposure is sub-maximal, sessile intertidal species invade the infratidal fringe in force and penetrate to well below E.L.W.S. level.

Emergence ceases at about M.L.W.S. level on a moderately exposed rock and below this the vertical changes in the biota are gradual. The infratidal work has not been analysed by the method of critical levels for several reasons, chiefly because the transects have not covered a great enough depth range and the precise limits are known of too few species. The obvious changes, or critical levels, can be readily seen on the distribution diagrams, and an elaborate analysis would imply, in this case, a bogus precision.

A glance at figures 9 and 11 shows that, so far as exposed rocks are concerned, the depth of 1-2 metres is important as the lower limit of many intertidal species and the upper limit of infratidal species which dislike turbulence (note that they will rise above datum in very sheltered places). This level corresponds with the lower limit of influence of cascading water here. Lower down at 4-5 metres are the lower limits of many species that are very characteristic of the fringe and the upper limit of one

species that, on the contrary, is certainly not a typical species of the fringe. The change at this level is possibly due to the decrease of turbulence to negligible importance as a limiting factor: it is likely that lesser depths are subjected to cascading when the swell is very heavy. But the deduction of critical levels from only one or two transects of small depth range, such as these, is unsatisfactory: one knows that species which here go no deeper than, say, 4 metres are found on other rocks at 12 metres (e.g. *Pyura*).

A comparison of shallow and deep sites shows that algae become negligible in importance between 7 and 10 metres depth but this important change is not shown by any one transect. It is interesting that when light is kept from shallow rocks, such as within a cave, the fauna is apparently not the same as that of deep rocks which are dimly illuminated. This shows the effect of factors such as turbulence and temperature.

Drach (1948a) has exclaimed on the patchy distribution of species on infratidal rocks in European waters and aptly describes it as 'a mosaic difficult to analyse'. It has been shown here that much of the patchiness is due to the effects of turbulence and illumination cutting across the vertical changes. But the rocks at 11-17 metres also showed patchiness which, in their case, could not be ascribed either to turbulence or illumination. Possibly it is due to intense inter-specific competition.

Drach emphasizes that infratidal rocks are totally colonized and deduces that the most stringent environmental influence is that of competition for space. Certainly, as soon as the rock is 100 per cent colonized, competition is very important in determining the balance between the species that other environmental factors permit to be present. It is possible that patchiness increases with inter-specific competition and indicates its intensity. Eyre (1939) and Stephenson *et al.* have remarked on the great patchiness in the lower parts of the intertidal region and in the infratidal fringe. At these levels, the competition for space is intense and the biota reflect very sensitively the slightest differences in the environment. Higher levels are not 100 per cent colonized (and so competition is less) and are less patchy. Stephenson (1939, 506) remarks that, intertidally, 'horizontal differentiation appears to affect the lower zones more markedly than the upper'. Patchiness is certainly great to 17 metres depth, as might be expected from the total colonization of the rocks, but it is undoubtedly greatest in the shallows where changes in turbulence and other factors are more pronounced.

It is felt that there is probably an intrinsic patchiness everywhere due to inter-specific competition and the vagaries of mortality and spat-fall but that in the shallows, say, at less than 6 metres, patchiness is increased by the different environmental factors.

It is interesting to compare very briefly this work in False Bay with that of biologists elsewhere.

The analysis of intertidal critical levels can be compared with the work of Colman (1933) and of Evans (1947) at Plymouth, and of Knox (1953) in New Zealand. In their analyses Colman and Evans considered twenty-two species and Knox thirty-four and so the analyses of the Exposed and Semi-exposed transects in this paper should be comparable. For the other two False Bay transects the number of important

species is probably too low for a good analysis. In the following discussion, the Shady, Very Sheltered site is disregarded because of the complication of shading.

At the outset the problem arises whether true (predicted) tidal levels should be considered (as was done by Evans and by Knox) or whether allowance should be made for wave upwash, giving 'effective' levels (*vide* Colman). The argument for using effective levels is persuasive. Figure 6 shows the rise of species with increasing upwash and figure 8 shows that allowance for upwash adjusts the critical levels to about the same effective heights so far as the highest ones are concerned. But this does not hold at all for the lowest critical levels, as has been mentioned, and figure 8 shows that wave action affects the pattern of critical levels markedly. This last point contrasts with the data of Evans who shows that the arrangement of the critical levels at five localities at Plymouth (his fig. 14) is very similar despite their exposure ranging from 'Very exposed' to 'Very sheltered' (his Table I). Since for False Bay the effect of wave action is not simply to raise everything up a rock, and since it is difficult to work with mental pictures of effective levels for different sites, it is suggested that it might be best to work relative to true levels always, provided an estimate of upwash is also made. Although Knox works with true levels it seems that they are also effective levels because he discounts the effect of wave action by his choice of locality and in his field observations.

It is interesting to find Knox in agreement with Evans as to the most critical levels (M.L.W.N. to M.L.W.S. and E.H.W.N. to M.H.W.S.) and the least critical level (around M.S.L.) even though their localities are so widely separated. Colman's results are very similar when his wash-allowance has been discounted. On the other hand, the critical and uncritical levels of the False Bay intertidal show no agreement with these. A feature of the False Bay transects is the uncritical zone from true E.L.W.S. level to about 0.5 metre deeper which was too deep for consideration by the other workers.

It might be supposed that the percentage emergence curve, which varies according to the tidal characteristics of different localities, would be linked with the critical biological levels. Knox finds this to be so for he finds the most critical levels to occur where the greatest rate of change of emergence is found. On the other hand, neither Colman nor Evans finds such a correlation. The analysis of False Bay work shows no critical level to correspond with the upper inflection of the curve but the level of the lower inflection is consistently critical. It is recalled that the upper inflection, at M.H.W.S., appears to be important biologically even although this does not appear from the analysis. It is the upper limit of barnacles.

It is felt that the concept of critical biological levels is very useful but that the method of application of the concept requires investigation on mathematical and interpretive grounds. Several serious drawbacks of the analysis, as it stands, have been mentioned above. It is also apparent that the degree of 'criticalness' should be mathematically defined for there is a danger of every level of the intertidal being described as notably critical or notably uncritical without nondescript levels being recognized. Colman noted three critical zones and one uncritical zone for an extreme spring tidal range of about 19 feet at Plymouth, and later Evans recognized five

critical zones and one uncritical for the same place. Knox, dealing with an extreme spring range of about 9½ feet, describes six critical zones and one uncritical zone. The extreme spring range in False Bay is 7 feet and it would have been surprising to find so many critical levels.

The datum chosen for this work in False Bay is 0.09 metre (3.55 in.) above M.L.W.S. and it is worth while to discuss its suitability as the dividing line, by definition, between the intertidal and infratidal regions. Of course, strictly speaking, the intertidal region extends to E.L.W.S. which is 0.33 metre (13.15 in.) below datum, which agrees closely enough with the datum levels chosen by Colman and by Evans ('Chart Datum', which is about 0.2 ft. below M.L.W.S.) and by Knox ('Chart Datum', which is at 0.4 ft. above M.L.W.S.). However, the analysis for critical levels shows that datum level, or just above it, is the most consistently critical level on the shore. Hereabouts are found the lower limits of many intertidal species and the upper limits of many infratidal species. The upper limit of the infratidal fringe is either at datum, or above it, and it has been concluded above (p. 435) that the upper boundary of the fringe is the biological boundary between the inter- and infratidal regions. Therefore, although the datum may be odd and the terminology poor, it definitely gives the truest picture of the biological changes. It will be noted that the infratidal fringe is the topmost edge of the infratidal region, as defined here; whereas according to Stephenson's terminology (1939, p. 512) it is the lowest part of the intertidal region.

Regarding the infratidal biota there is little work of this type for comparison. Recently Forster (1954 and 1955) has given descriptions of localities on the English Channel which, although the author has no experience of the infratidal there, are surprisingly familiar in the light of his knowledge of False Bay. It is remarkable that the biotic pattern appears to be similar infratidally in the Plymouth area and in False Bay. Most of the species mentioned by Forster are matched by similar ones—often of the same genus—in False Bay. Indeed, the alga *Dictyota dichotoma* is present both at East Blackstone, off Dartmouth, and in False Bay, and covers a similar depth range. Forster's descriptions also reveal the presence of vertical distribution gradients in place of sharp vertical zonation and they make it clear that distribution is extremely patchy (at any rate for East Blackstone between 6 and 18 metres).

Algae obviously dominate the shallows at all of Forster's localities and he finds the change to dominance by animals at about 25 metres in the clear water at Stoke Point and, apparently, at about 8 metres in the turbid and sheltered waters at East Blackstone. It will be recalled that algae were conspicuous at Oatland Point on the Channel bottom at 6 metres but virtually absent near Roman Rock at 11 metres, both localities having a water clarity of about the order of that at Stoke Point. Of course, close comparison is not possible because of the dominance of the kelp *Laminaria* in the Plymouth area and the merely 'fairly common' abundance of the kelp *Ecklonia* in the Oatland Point/Roman Rock area. A kelp profoundly affects the biota of the rocks beneath because of its size (commented upon by Kitching, 1941) and the shallows in the Plymouth area are obviously covered in kelp forest, whereas at Oatland Point the kelp is short and never forms a forest. In the south of False Bay where

great forests of *Ecklonia* are to be found they profoundly affect the biota. These *Ecklonia* forests have been observed to extend certainly as deep as 10 metres and probably to 15 metres, which is on par with Forster's lower limit of *Laminaria* at 17 metres. But dredging operations suggest that it is unlikely that algae in numbers extend deeper than 15 metres in False Bay whereas Forster comments on algae being common as deep as 25 metres. It is a somewhat surprising detail to find algae extending deeper in the Plymouth area (latitude about $50\frac{1}{2}^{\circ}$ N.) than in False Bay (latitude about $34\frac{1}{2}^{\circ}$ S.) when water clarity is of the same order. It is interesting that Forster lists coelenterates and polyzoa as the commonest of the animal groups just below the algal belt, both at Stoke Point and at East Blackstone. Both groups have been noted as very important and characteristic in the cave at Oatland Point and coelenterates were particularly important on open bottoms deeper than 11 metres.

Kitching, Macan and Gilson (1934) also studied the infratidal region on the south Devonshire coast, working down to 3 metres depth below M.L.W.S. level. They found that open, sloping rock faces were dominated by algae, chiefly by *Laminaria* forest, which agrees with Forster's later results. They found overhanging slopes supporting an entirely different association—one in which *Laminaria* was virtually absent and which was dominated instead by the ascidian *Distomus* and the sponge *Halichondria*, with other sponges and many hydroids. This association recalls the biota of the cave at Oatland Point. They discuss the importance of the slope of a rock and stress the associated factors of illumination, of settling potential for spores and of silt deposition. They suggest that freedom from silt deposition is particularly responsible for many of the peculiarities of the *Distomus-Halichondria* association, in particular for the importance of sponges, coelenterates and ascidians. This is interesting but no similar suggestion is advanced for these groups of animals in False Bay. It is felt, rather, that these groups are among the commonest in the shallow infratidal and so are most likely to colonize a rock face not dominated by algae. They make the interesting observation that the lack of large, brown algae (e.g. kelp) from this association is not due to insufficient illumination but to other factors, possibly the inability of their spores to settle.

Kitching *et al.* also note that barnacles are rapid colonizers of bare rock but are rapidly overgrown later. They comment on the common occurrence of barnacles in the intertidal and at the base of gullies where strong scouring probably occurs. It will be remembered that dead barnacle shells were a common feature of the rocks at Noah's Ark and at two of the Roman Rock sites while live *Balanus* were common at the third Roman Rock site, but it is most improbable that scouring is a common occurrence at any of these places.

Kitching (1941) finds that on the west coast of Scotland the shallow infratidal is, again, dominated by laminarian forest down to at least 15 metres. The species there are different from those off Plymouth, in general, and of course there are detailed differences in zonation. It is particularly interesting to find from his account that the algae of the infratidal fringe differ from those of the truly infratidal zone. Kitching emphasizes the sharp drop in illumination from the infratidal fringe to

within the *Laminaria* forest just below it due to shading by the kelp. These points together suggest that the infratidal fringe there possesses a character unlike the true infratidal which is strikingly different from the situation in False Bay. In an endeavour to explain this difference, it is worth recording that Kitching states (p. 335): 'At the upper margin of the sublittoral region, exposed to air at low water of spring tides, there is a characteristic "sublittoral fringe".' This and relevant sentences elsewhere imply that the upper margin of the infratidal fringe is a little above M.L.W.S. level and possibly detailed work on tidal levels will show that Kitching's 'sublittoral fringe' corresponds to the lowest level of the intertidal zone by the definitions used here. For instance, Kitching's figure 1 shows that of the species around datum level (presumably M.L.W.S.) five extend upwards from datum, four extend downwards from datum and only two others really overlap on either side of datum. In other words, so far as his figure 1 is concerned, datum seems to divide the intertidal from the infratidal very well and his datum seems pretty much the same as my datum.

Although Kitching deals with a kelp forest his conclusions are similar to those for False Bay in that the 'zonation' (vertical distribution gradients) of the infratidal region depends upon wave action and illumination. Kitching reaches this conclusion after pointing out the uniformity in the illumination, and in the constitution of the undergrowth of the forest, over a vertical range of at least 12 metres. Kitching also discusses briefly the vertical succession in English waters of green, brown and then red algae, and it is noteworthy that this sequence is not found in False Bay. Algae of all three groups are mixed at almost any level here and reds occur abundantly in the intertidal and shallow infratidal whether the illumination is modified by kelp or not.

It is clear that the infratidal localities in England that have been mentioned show many features in common with the infratidal of False Bay. Further diving in different latitudes would be extremely interesting.

It seems that interpretation in terms of vertical zonation must be abandoned for shallow infratidal work, and instead it is suggested that the best approach would be in terms of communities (as for soft bottoms) and their intergradation vertically and horizontally. There is a great need for autoecological work and for experiments to determine precisely the tolerances of various species to the different features of illumination and of wave action. False Bay species that would be particularly interesting are *Ecklonia*, *Pyura* and the *Lithothamnium*.

SUMMARY

The biotas of four intertidal, rocky transects were examined relative to surveyed levels and examination was continued below the intertidal zone by means of diving. Biotic differences between the transects are discussed, particularly in relation to exposure to wave action, and an analysis of critical levels is made and criticized.

Eleven infratidal rocky sites were examined by means of diving to a maximum depth of 17 metres. The sites included vertical faces, flat and sloping rocks of the bottom and a shallow cave. The biotas were examined in terms of vertical zonation for comparison with the intertidal transects.

The main changes in emergence, lighting and turbulence as one drops from the top of the intertidal region to 17 metres depth and the effects on the biota of these changes are considered.

In the Discussion, the changes that are seen in the biota are discussed more generally and are compared with work in European waters and in New Zealand. The intertidal critical levels of False Bay show little correspondence with those elsewhere but the shallow infratidal biology has some striking similarities to that in England⁵ and Scotland.

It is suggested that the selected datum (or, alternatively, M.L.W.S., which is $3\frac{1}{2}$ inches below it) is very suitable as the boundary by definition between the intertidal and infratidal regions. The biological boundary is clearly at the upper limit of the species of the infratidal fringe.

It is recommended that intertidal zonation should be related to actual (or predicted) tidal levels, not to 'effective' levels, provided that estimates of wave upwash be given. Infratidal work should be examined in terms of communities and their modification under the stress of different environmental features rather than in simple terms of vertical zonation.

ACKNOWLEDGEMENTS

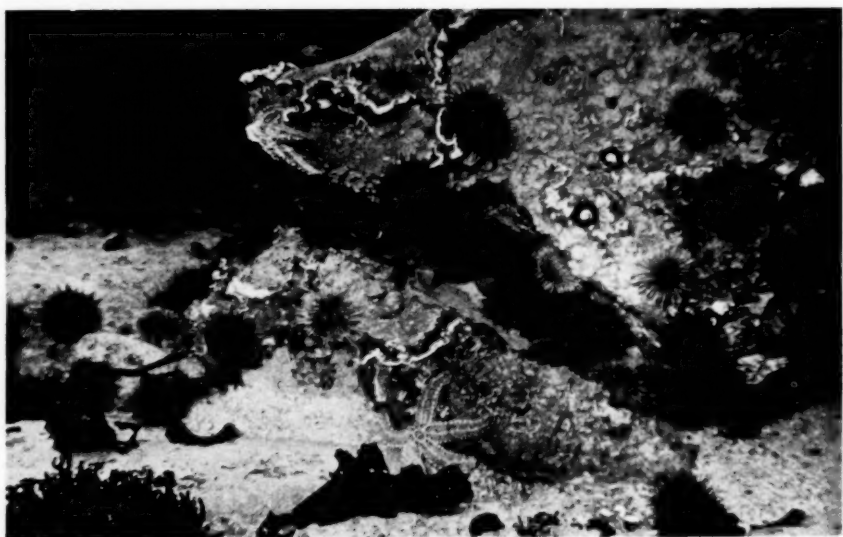
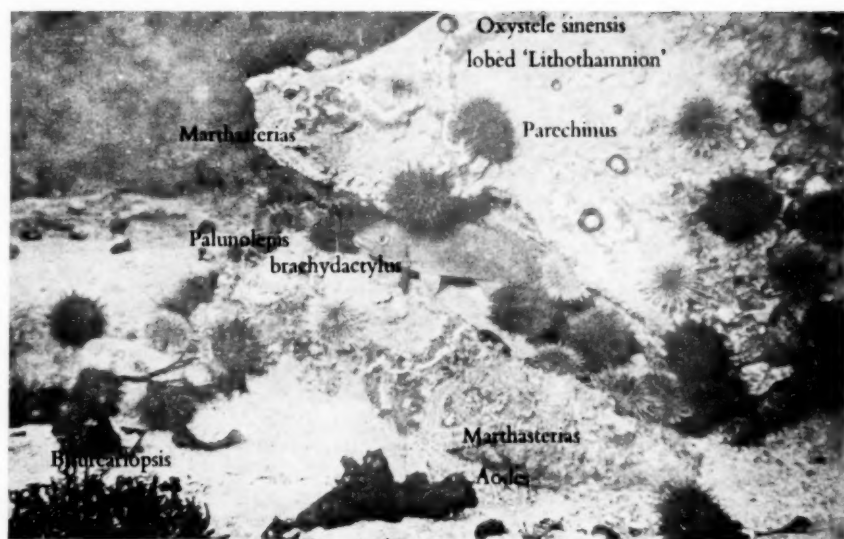
It is a pleasure to acknowledge my debt to Professor J. H. Day whose Research Assistant I was at the time that the field-work was done for this paper. Professor Day grudged me neither time nor facilities and I owe much to his friendly advice and stimulation from beginning to end. I acknowledge, too, permission from the Council for Scientific and Industrial Research, whose funds provided Professor Day with a Research Assistant, to undertake this work in addition to my duties in estuarine research. C.S.I.R. went further and made a grant for the purchase of the necessary diving apparatus. The University of Cape Town made a staff research grant under which an excellent camera and electronic flash were bought and their underwater housings were constructed for me by the Physics Department workshop. A diving-suit was also made available by a staff research grant. Indispensable help was given by friends too numerous to mention and who will, I hope, accept this brief note of thanks.

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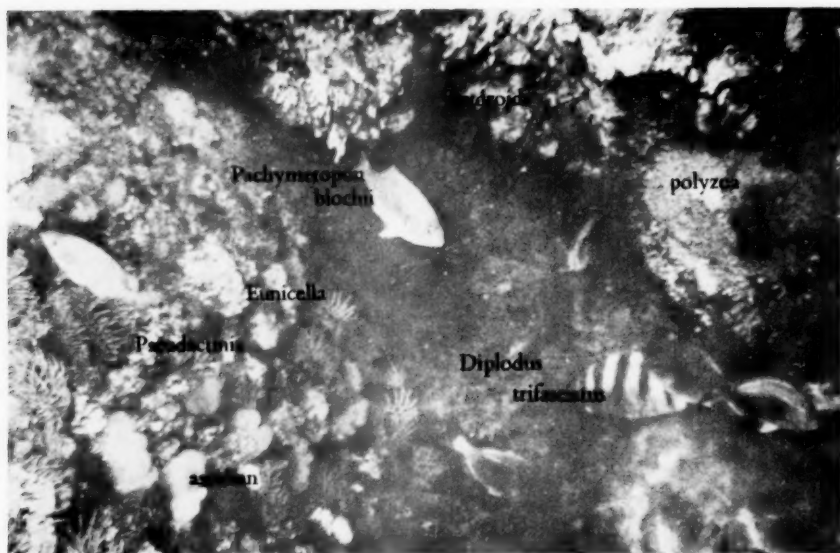
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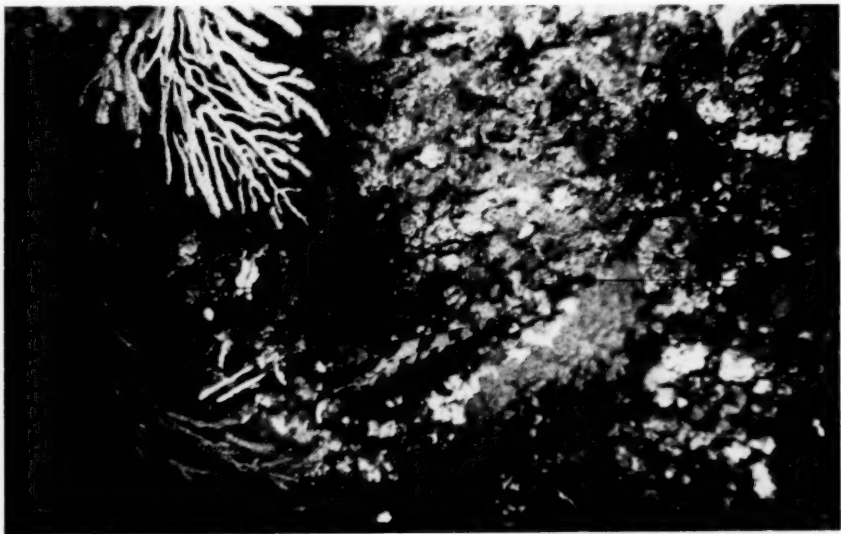
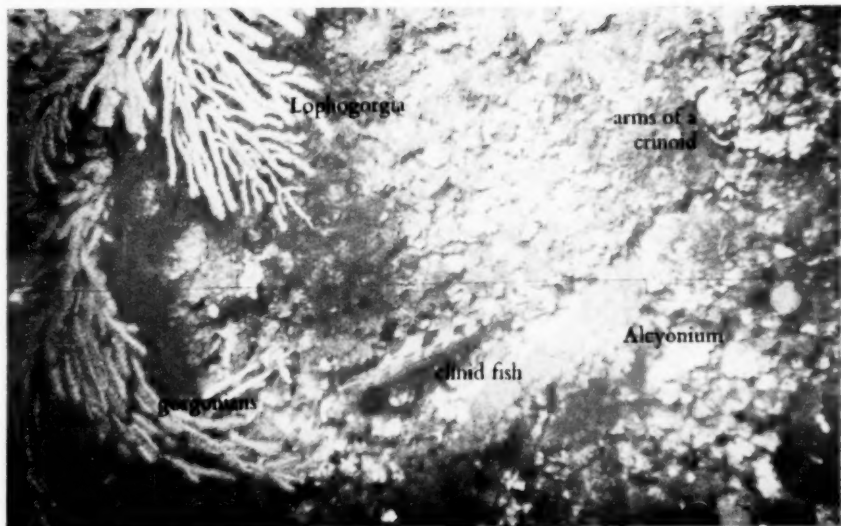
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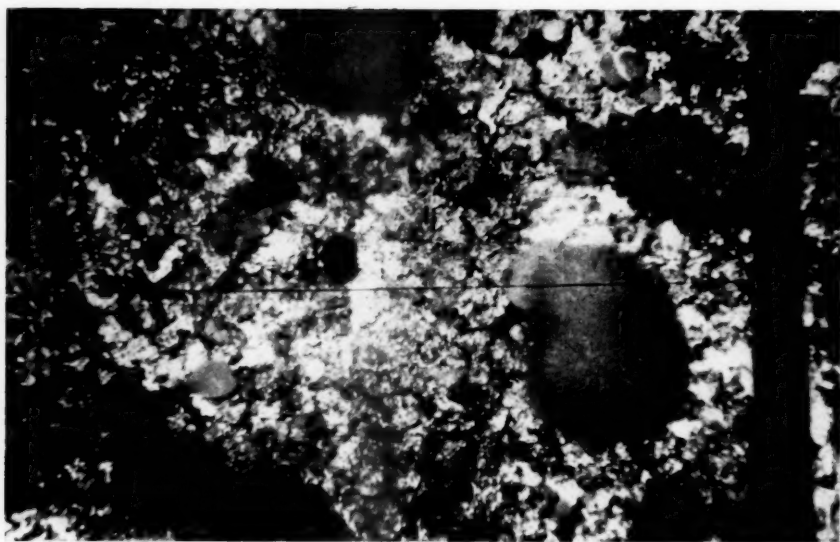
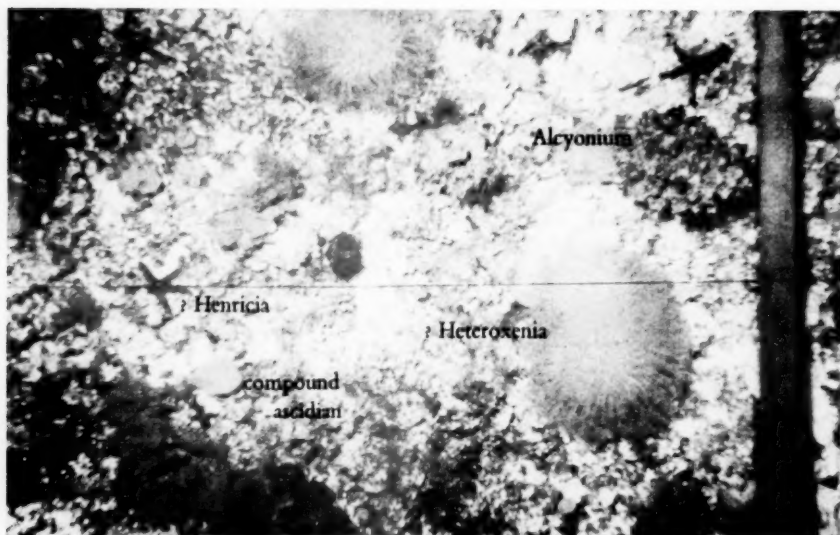
The Lagoon Bottom. A very characteristic scene.



At 4 metres depth within a cave, Oatland Point. The cave was dimly lighted; a darker recess is shown in the background of the picture. The cave is situated on the north-eastern side of the Channel under a conical rock (shown as rather square, in plan view, in fig. 2).



A cave wall at 2 metres depth. The cave is the same as that of Plate XX. The wall overhangs at about 75° to the horizontal and is rather dimly lighted. The black line across the photo is due to a scratch caused by a defect in the camera.



A cave wall at 2 metres depth. This photograph was taken next to that of Plate XXI. The focus-stick is seen in this photo; it is marked in decimetres and the markings can just be seen at its left margin. The height of the photograph corresponds to 45 cm. on the rock.

NOTES ON THE PHYTOGEOGRAPHY OF THE FLORA OF THE CAPE PENINSULA

By R. S. ADAMSON

(Read March 19, 1958)

A sample of the flora of the Cape Peninsula is analysed phytogeographically. The flora is divisible into that of the mountains and that of the Cape Flats. In distribution of the species the mountain flora shows signs of great age. In part it is related to a climate moister than that existing. The Flats flora is more modern.

The unique flora of the south-west Cape Province has been the subject of much phytogeographical work and speculation. In recent years a firm basis for such studies has been laid by Levyns (1938, 1952) and by Weimarck (1941). Both authors have reached the conclusion that the flora as a whole is ancient and is one that now occupies a smaller area than it did at one time. The diminution of area has been brought about by increasing dryness of the climate. Though reduced in area, the flora has been one in which species differentiation has been active.

In most of the work that has been carried out the flora as a whole has been dealt with. There have been a number of studies of individual genera and some numerical comparisons of local floras but up to the present little has been attempted in the phytogeographical analysis of any small area. For such a purpose the Cape Peninsula is a most suitable unit. It is distinct geographically and its flora has been studied in some detail. The present paper is merely preliminary but even as such it is hoped that it may stimulate others to undertake more intensive work.

THE CAPE PENINSULA

In the *Flora of the Cape Peninsula* (1950) the boundaries of the area were taken as those parts covered by the set of maps issued by the Trigonometrical Survey in 1933. In the present study a rather larger portion of the Cape Flats is included. The boundaries taken are a line drawn half-way between the mountains on the Peninsula and those on the mainland, and a line through the centre of Table Bay.

The general features of the Cape Peninsula are so well known that no repetition of them is called for here. A clear account is available in *The Cape Peninsula* edited by J. A. Mabbitt (1952) where in addition there is given a sketch of the past history of the region. In brief the Peninsula is a promontory about 35 miles long and up to 5 miles across which is connected to the mainland by the low-lying plain of the Cape Flats. In the opening words of the handbook quoted 'a relief map conveys an

immediate impression of an island'. The 'island' consists of a range of mountains or hills extending from Table Mountain in the north with decreasing altitudes southwards to Cape Point. The range is interrupted by the low valley between Fish Hoek and Kommetjie and to a less extent by the narrow col at Constantia Nek. These mountains are a detached part of a very ancient land surface that has remained stable since Jurassic times. There have been changes in elevation of the land but no other major alterations. The existence of raised beaches indicates an elevation sufficient to have raised the Cape Flats above sea level.

THE FLORA

In any attempt to unravel the phytogeographical relations of a flora it is necessary to know the distribution of the component species both on the area studied and outside. To do this for the whole of the flora of the Peninsula would be a most laborious task. The 'Flora' enumerates over 2,600 species. Even if all alien and doubtfully indigenous species were omitted the total is still a formidable one. To get round this difficulty the present study is based on a sample made up of a number of genera which have been revised within recent years. This is a method that was used by Weimarck (1941) in his analysis of the distribution of the Cape flora as a whole.

The sample chosen for this study is not identical with that used by Weimarck though it contains many of the same plants. It comprises 393 species in 44 genera. It consists of:

Genus	No. of species	Genus	No. of species	Genus	No. of species
<i>Adenogramma</i>	.. 4	<i>Elegia</i> 18	<i>Pharnaceum</i> 8
<i>Agathosma</i> 12	<i>Elytropappus</i> 5	<i>Phytica</i> 20
<i>Aloe</i> 4	<i>Galenia</i> 6	<i>Polpoda</i> 1
<i>Aristea</i> 12	<i>Gibbaria</i> 1	<i>Polygala</i> 9
<i>Arthrocnemum</i> 6	<i>Hypertelis</i> 2	<i>Prismatocarpus</i> 3
<i>Audouinia</i> 1	<i>Hypodiscus</i> 4	<i>Pseudobaeckia</i> 1
<i>Berzelia</i> 3	<i>Hypolaena</i> 4	<i>Restio</i> 29
<i>Brunia</i> 1	<i>Juncus</i> 19	<i>Roella</i> 10
<i>Cannamois</i> 1	<i>Leptocarpus</i> 7	<i>Salicornia</i> 1
<i>Centella</i> 16	<i>Lightfootia</i> 7	<i>Staavia</i> 4
<i>Chondropetalum</i> 8	<i>Lobostemon</i> 9	<i>Staberoha</i> 4
<i>Chrysanthemoides</i> 2	<i>Metastasia</i> 6	<i>Stoebe</i> 11
<i>Cliffortia</i> 30	<i>Mollugo</i> 1	<i>Tetragonia</i> 8
<i>Coelanthum</i> 1	<i>Muraltia</i> 25	<i>Thamnochortus</i> 10
<i>Dimorphotheca</i> 3	<i>Ornithogalum</i> 10	<i>Willdenowia</i> 6
<i>Disparago</i> 3	<i>Oxalis</i> 32		

(NOTE.—In this and all subsequent lists the plants are arranged alphabetically.)

A sample of this size is clearly too small for statistical analysis but it is sufficient to bring out general features. It can be taken as representative of the flora as a whole though it does not contain any forest plants which present special geographical problems. The sample contains genera which have the main concentration of their species in or about the Caledon division and some which do not exhibit this feature.

The former have been looked on by Levyns (1952) as being the true members of the Cape flora, the others as invaders from some other flora. Examples of the latter are such genera as *Aloe*, *Pharnaceum*, *Polygala* or *Tetragonia*. Some genera stand in an intermediate position, e.g. *Juncus* or *Lightfootia*. Both are widespread genera but in both there are sections which exhibit the characteristic concentration of the true members of the Cape flora.

The delimitation of species and their distribution areas have been taken from the various monographs. Though the data have been supplemented where possible by field observation and from herbaria, this has not been undertaken for all the species. Distribution on the Peninsula itself has been checked as far as possible by field observation and by reference to herbaria.

DISTRIBUTION ON THE PENINSULA

As regards both flora and habitat conditions the Peninsula is divisible into two parts: the mountains and the sandy flats. However, as these two regions are of very unequal size, the mountain part has been divided into three sections for convenience in noting distributions. Thus, for the purpose of this paper the Peninsula is divided into the following four sections:

1. Table Mountain to Constantia Nek.
2. Constantia Nek to the Fish Hoek-Kommetjie Valley.
3. The southern Peninsula.
4. The Cape Flats.

These sections are not by any means strictly natural areas. Coasts are common to all. Areas such as the flats at Chapman's Bay are included in section 2 though both in habitat and flora much more nearly allied to the Cape Flats. Making allowance for such anomalies, the sections are a convenient and simple means of recording distribution.

If the sample is analysed the results are, as might be expected, that the largest numbers of species are restricted to a single section with lesser numbers as the number of sections is increased. The actual figures are 161 (40%) in a single section, 95 (24%) in 2, 76 (19%) in 3, and 61 (16%) in all four.

Of the sections 1 is the largest, has the greatest range in altitude and the greatest variety in habitat, and has the largest flora and the greatest number of species not found in other sections. Figures showing the distribution by sections are:

Section	Total sp.	Peculiar sp.	Species common to sect.			
			1.	2.	3.	4.
1.	225	66	-	129	118	112
2.	172	11	129	-	118	100
3.	192	28	188	188	-	110
4.	209	56	112	100	110	-

When allowance is made for inequalities in size of the sections and for other features mentioned earlier, these figures show that the flora is distributed without

any centre of concentration. They also bring out the absence of any special agreement between adjacent sections. There are as many species in common between sections 1 and 3 as between either and the intervening section. From these figures there is no evidence for any definite path of movement along the Peninsula. Such features are brought out even more clearly when a small group of species is treated in the same way. The species endemic to the Peninsula, which number 52, form a suitable example. Analysis of these shows that only 1 is found in all four sections, 3 occur in 3 sections, 13 in 2, and 37 in one section only. Their distribution through the sections is shown in the following table:

Section	Total	Peculiar	Common to sect.			
			1.	2.	3.	4.
1.	22	14	—	6	6	1
2.	15	3	6	—	8	3
3.	23	12	6	8	—	7
4.	12	8	1	3	7	—

COMPARISON WITH THE MAINLAND

As the Cape Peninsula forms a small promontory it is to be expected that its flora will be closely similar to that of the mainland. There are, however, a number of differences. No fewer than 52 species or almost 13% of the sample are endemic to the Peninsula. There are also many species which are abundant on the mainland but wanting on the Peninsula. Among these are:

<i>Agathosma anomala</i> E. Mey. ex. Steud.	<i>Muraltia aspalatha</i> DC.
<i>A. crenulata</i> (L.) Pillans	<i>M. filiformis</i> (Thb.) DC.
<i>A. juniperifolia</i> Bart.	<i>Muraltia rosmarinifolia</i> Levyns
<i>A. odoratissima</i> (Mast.) Pillans.	<i>M. serpylloides</i> DC.
<i>A. virgata</i> (Lam.) Bart. & Wedd.	<i>M. trinervia</i> (L.f.) DC.
<i>Aristea lugens</i> (L.f.) Ker.	<i>Osteospermum junceum</i> Berg.
<i>A. oligocephala</i> Baker.	<i>O. scariosum</i> DC.
<i>A. racemosa</i> Baker	<i>Phyllica lasiocarpa</i> Sond.
<i>Brunia arachnoides</i> (Wendl.) E. & Z.	<i>Prismatocarpus diffusus</i> (Thb.) A.DC.
<i>Centella calliodus</i> (Cham. & Schl.) Adamson	<i>Restio callistachyus</i> Kunth
<i>Hypodiscus argenteus</i> (Thb.) Mast.	<i>R. curviamis</i> Kunth
<i>H. striatus</i> (Kunth) Mast.	<i>R. laniger</i> Kunth
<i>Leptocarpus hyalinus</i> (Mast.) Pillans	<i>R. purpurascens</i> Nees
<i>Lobostemon echinoides</i> Lehm.	<i>R. subverticillatus</i> Mast.
<i>Metalsia Lichtensteinii</i> Less.	<i>Roella incurva</i> A.DC.
<i>M. seriphifolia</i> DC.	<i>Staberoha aemula</i> (Kunth) Pillans

In addition to these there are a number of species which are common on the mainland but rare or restricted on the Peninsula. Among these are:

<i>Adenogramma mollugo</i> Reichb. f.	<i>Muraltia brevicornu</i> DC.
<i>Agathosma tabularis</i> Sond.	<i>M. pauciflora</i> (Thb.) DC.
<i>Centella difformis</i> (E. & Z.) Adamson	<i>Ornithogalum lactum</i> Jacq.
<i>C. flexuosa</i> (E. & Z.) Drude	<i>O. pilosum</i> L.f.
<i>C. scabra</i> Adamson	<i>Osteospermum imbricatum</i> L.
<i>C. triloba</i> (Thb.) Drude	<i>O. tomentosum</i> (L.) Norl.

C. villosa L.
Cliffortia eriocephala Cham.
C. ilicifolia L.
C. marginata E. & Z.
Elegia verticillaris Kunth
Galenia africana L.
Gibbaria ilicifolia (L.) Norl.
Lightfootia oppositifolia A.DC.
Muraltia alopecuroides DC.

Pharnaceum dichotomum L.f.
Phylica atrata Link ex R. & S.
P. disticha E. & Z.
P. nigrita Sond.
P. pubescens Ait.
Pseudobacckia africana (Burm.) Pillans
Restio ochreatus Kunth
Tetragonia spicata L.f.

Of the above, four species, *Pharnaceum dichotomum*, *Phylica atrata*, *P. disticha* and *P. nigrita*, have been recorded from the Peninsula but have not been seen there for the past fifty years. In addition to the list above, two species *Centella virgata* (L.f.) Drude and *Cliffortia Dregeana* Presl are represented on the Peninsula by varieties only.

In contrast to the above a number of species appear to be much more common on the Peninsula than they are on the mainland. Such are:

Agathosma Hookeri Sond.
Centella hederacfolia (Burch.) Drude
Elegia Neesii Mast
Lobostemon montanus (DC.) Buek
Phylica dioica L.
P. strigosa Berg.
Prismatocarpus nitidus L'Her.

Restio bifurcus Nees
R. Harveyi Mast.
R. Dodii Pillans
R. major Pillans
R. multiflorus Spreng.
R. quadratus Mast.
Roella muscosa L.f.

Of the above list three species are represented outside the Peninsula by varieties only. In no case has the variety been recorded on the Peninsula.

GEOGRAPHICAL COMPONENTS

When the distributions of the species are plotted on maps a great variety of pattern results. These patterns can be grouped together in accordance with their general similarities into components. Such grouping was first carried out by Weimarck (1941) for the Cape flora as a whole. As here attention is focused on the Cape Peninsula, a rather different scheme is adopted. Five components are recognized. These are:

Endemic. Species confined to the Cape Peninsula.

South-western. Species occurring on the Peninsula and on the mainland immediately adjoining. The extreme boundaries are the Paarl-Wellington mountains in the north, the Caledon-Bredasdorp hills on the east. None of the species occur north of the Brede River and very few east of the Bot River. This component corresponds generally with Weimarck's 'south-western endems'.

Northern. These are species with a range extending northwards but not to the east on the coastal ranges. This corresponds to Weimarck's 'western group'.

Eastern. These are species which range along the south coast but do not extend northwards. It overlaps the south-western component but the eastern extension is greater. In it are included both Weimarck's 'southern group' and 'Langeberg-south-western endems'.

Wide. These are species that extend both north and east from the Peninsula. Most of the plants here would be included in Weimarck's 'Cape ubiquists'.

In any such scheme as this it must be realized that the components are not at all sharply marked off and personal judgment often comes into play in the placing of

a plant in one or another. Allowing for such borderline cases the species can be grouped under the components as follows:

Total	Wide	S.W.	East.	North.	Endem.
393	143	93	48	57	52

Distribution maps for many of the species in the sample have been published by Leighton, Levyns, Norliandh and Weimarck. None are considered as necessary here.

In dealing with the species as represented in the geographical components the mountain flora and that of the flats are treated separately.

MOUNTAIN FLORA

This is the larger part and includes the plants growing on the hills and mountains of the Peninsula together with those on the flat areas in the south. It contains representatives of all the components.

Endemic. The following endemic species are mountain plants:

<i>Agathosma lanceolata</i> Engl.	<i>Muraltia satureoides</i> var. <i>Salteri</i> Levyns
<i>A. pulchella</i> Link	<i>M. stipulacea</i> (Burm.) Levyns
<i>Aloe commixta</i> Berg.	<i>Phylica Schlechteri</i> Pillans
<i>Aristea rigidifolia</i> Lewis	<i>Polygala recognita</i> Chodat
* <i>Cliffortia Theodori-Freisii</i> Weim.	<i>Restio communis</i> Pillans
* <i>Elegia fenestrata</i> Pillans	<i>R. cincinnatus</i> Mast.
<i>E. intermedia</i> (Steud.) Pillans	<i>R. pusillus</i> Pillans
<i>Hypodiscus palustris</i> Pillans	<i>R. sarcocladus</i> Mast.
<i>Leptocarpus ramosissimus</i> Pillans	* <i>Roella amplexicaulis</i> W.-Dod
* <i>Lightfootia longifolia</i> A.D.C. var. <i>corymbosa</i>	<i>R. decurrens</i> L'Her.
Adamson	* <i>R. Goodiana</i> Adamson
<i>L. tenuis</i> Adamson	<i>R. recurvata</i> A.D.C.
<i>Muraltia acipetala</i> Harv.	<i>R. squarrosa</i> Berg
<i>M. curvipetala</i> Levyns	<i>R. triflora</i> (Good) Adamson
* <i>M. brachypetala</i> W.-Dod	<i>Staavia Dodii</i> Bolus
* <i>M. Comptonii</i> Levyns	<i>Staberoha vaginata</i> (Thb.) Pillans
* <i>M. demissa</i> W.-Dod	<i>Stoebe rosea</i> W.-Dod
<i>M. diabolica</i> Levyns	<i>Thamnochortus Levynsiae</i> Pillans
* <i>M. mixta</i> (L.) DC.	<i>T. nutans</i> (Thb.) Pillans
* <i>M. orbicularis</i> Hutch.	<i>T. plumosus</i> Pillans
<i>M. Pageae</i> Levyns	* <i>T. sporadicus</i> Pillans

Not all these endemics are of one category. Some of them (marked by an asterisk *) appear as differentiations from other species which are for the most part more widespread. These should be regarded as relatively recent differentiations which have not spread out from their place of origin. A rather extreme example is seen in *Roella Goodiana*. This is very closely allied to *R. recurvata* and is confined to one small area in the southern Peninsula. It is most probably a quite recent mutation. By contrast others are taxonomically rather isolated species and in some cases regarded as rather primitive in the genera. Among such are: *Agathosma pulchella*, *Aristea rigidifolia*, *Hypodiscus paludosus*, *Phylica Schlechteri*, *Restio cincinnatus*, *R. communis*, *R. pusillus*, *Roella recurvata*, *Staberoha vaginata*, *Stoebe rosea* and *Thamnochortus Levynsiae*. These appear as old species that persist as relics.

In a somewhat intermediate position are such cases as *Aloe commixta* and *Roella triflora*. The former is nearly allied to *A. striata*, a species found in the Eastern Cape. The two seem to be differentiations from a common ancestor that have now become geographically widely separated. The extent of the separation points to a distant period when there was continuity. *Roella triflora* has similar relationships but much less extreme. It is closely allied to *R. Dregeana* and *R. psammophila* which are found on restricted but separate areas on the adjacent mainland. It seems clear that the three species had a common ancestor and that they are species that have been differentiated by isolation. In both cases the origination of the species must have been in the remote past. Similar features can be shown for many of the other endemics.

Northern. The northern component is relatively small. In it are:

- | | |
|---|---|
| <i>Aristea dichotoma</i> (Thb.) Ker | <i>Oxalis lanata</i> L.f. |
| <i>Centella scabra</i> Adamson | <i>O. nidulans</i> E. & Z. |
| <i>C. villosa</i> L. | <i>O. versicolor</i> L. |
| <i>C. virgata</i> L.f. var. <i>gracilescens</i> Domin | <i>Polygala Lehmanniana</i> E. & Z. |
| * <i>Cliffortia Dregeana</i> Presl | <i>Pseudobaeckia africana</i> (Burm.) Pillans |
| * <i>Lightfootia oppositifolia</i> A.DC. | * <i>Restio ochreateus</i> Kunth |
| * <i>Lobostemon glaucophyllus</i> (Jacq.) Buek | * <i>R. perplexus</i> Kunth |
| <i>L. trichotomus</i> (Thb.) DC. | * <i>R. tenuissimus</i> Kunth |
| * <i>Ornithogalum lacteum</i> Jacq. | * <i>Willdenowia affinis</i> Pillans |
| * <i>O. hanodes</i> Leighton | * <i>W. luceana</i> Kunth |
| * <i>O. suaevoles</i> Jacq. | <i>W. striata</i> Thb. |
| <i>Oxalis commutata</i> Sond. | |

Of these species a considerable proportion (marked *) exhibit discontinuity in their distribution. This indicates a diminution of the one-time area occupied and points to the species being ancient members of the flora. A number of the species here are among those mentioned earlier as being restricted in distribution on the Peninsula. It is probable that for these the Peninsula represented the limit of their original range.

Eastern. This component is made up of plants which range along the south coast but not the west coast. The species fall into two groups: those with a more or less continuous range, and those which show discontinuities. The first group includes:

- | | |
|---|--|
| <i>Aloe saponaria</i> Haw. | <i>Elegia thyrsiflora</i> (Rottb.) Pers. |
| <i>Centella eriantha</i> (Rich.) Drude | <i>Osteospermum imbricatum</i> L. |
| <i>C. laevis</i> Adamson | <i>Oxalis caprina</i> L. |
| <i>Cliffortia ferruginea</i> L.f. | <i>O. punctata</i> L.f. |
| <i>C. filicaulis</i> Schltr. | <i>Phyllaea ericoides</i> L. |
| <i>C. odorata</i> L.f. | <i>Restio compressus</i> Rottb. |
| <i>C. pterocarpa</i> Weim. | <i>R. triflorus</i> Rottb. |
| <i>Elegia remosissima</i> (Poir.) Pers. | <i>R. triticeus</i> Rottb. |

Those with discontinuity include:

- | | |
|---|---|
| <i>Aristea pauciflora</i> W.-Dod | <i>Juncus sphagnetorum</i> (Buchen.) Adamson |
| <i>A. spiralis</i> (L.f.) Ker | <i>Leptocarpus paniculatus</i> (Rottb.) Pillans |
| <i>Chondropetalum muricatum</i> (Mast.) Pillans | <i>Restio dispar</i> Mast. |
| <i>Cliffortia falcata</i> L.f. | <i>Staavia glutinosa</i> Dahl |
| <i>C. ilicifolia</i> L. | <i>Stoebe sphaerocephala</i> Schltr. |
| <i>Juncus effusus</i> L. | |

The extent of the range of these species varies widely. In the list are a number of species which are characteristic of moist habitats. The absence of these along the mountains north of the Peninsula can be attributed to drought. The fact that a large proportion show gaps in their range points to these being ancient species and to restriction due probably to dryness. Some of the species exhibit very wide gaps. The case of *Staavia glutinosa* is included here on the strength of a single record from Van Stadens Gorge. Otherwise the plant is only known from the Peninsula where it is confined to Table Mountain.

South-western. This is a larger component. As already mentioned it is one which overlaps the previous two and is in many cases not at all easily separated. The species here can be divided into groups: those with more or less continuous distribution, and those with marked discontinuities. In both there are some species which extend over the whole area, some which are much restricted. For example, there are a number of species that are found only on the Peninsula and on the mountains adjoining the flats on the mainland. Species with a rather uniform distribution here are:

- | | |
|---|--------------------------------------|
| <i>Agathosma ciliaris</i> (L.) Druce | <i>Muraltia serpylloides</i> DC. |
| <i>Aloe socotrina</i> Lam. | <i>Oxalis argyrophylla</i> Salter |
| <i>Aristea macrocarpa</i> Lewis | <i>O. bifida</i> Thb. |
| <i>Centella difformis</i> (E. & Z.) Adamson | <i>O. falcata</i> Salter |
| <i>C. flexuosa</i> (E. & Z.) Drude | <i>O. lanata</i> L.f. |
| <i>Chondropetalum Hookerianum</i> (Mast.) Pillans | <i>O. monophylla</i> L. |
| <i>C. deustum</i> Rottb. | <i>O. tenuifolia</i> Jacq. |
| <i>Cliffortia dodecandra</i> Weim. | <i>Phyllica atrata</i> Licht. |
| <i>C. marginata</i> E. & Z. | <i>P. strigosa</i> Berg. |
| <i>Disparago laxifolia</i> DC. | <i>Prismatocarpus sessilis</i> A.DC. |
| <i>Elegia Neesii</i> Mast. | <i>Restio egregius</i> Hochst. |
| <i>Elytropappus longifolius</i> (DC.) Levyns | <i>Stoebe bruniades</i> Levyns |
| <i>Leptocarpus gra-tilis</i> (Mast.) Pillans | <i>S. cinerea</i> (L.) Thb. |
| <i>Lobostemon hispidus</i> (Thb.) Beuk | <i>S. incana</i> Thb. |
| <i>Lightfootia longifolia</i> A.DC. | <i>Thamnochortus gracilis</i> Mast. |
| <i>Metalsia cephalotes</i> (Thb.) Les. | |

Those with distinct discontinuities are:

- | | |
|---|--|
| <i>Agathosma ciliata</i> Link | <i>Leptocarpus membranaceus</i> Pillans |
| <i>A. Hookeri</i> Sond. | <i>Lobostemon montanus</i> (DC.) Buek |
| <i>A. tabularis</i> Sond. | <i>Muraltia rosmarinifolia</i> Levyns |
| <i>Aristea juncifolia</i> Baker | <i>Ornithogalum brevifolium</i> Leighton |
| <i>A. Zeyheri</i> Baker | <i>O. Schlechterianum</i> Schinz |
| <i>Audouinia capitata</i> Brongn. | <i>Osteospermum ciliatum</i> Berg. |
| <i>Centella carpitosa</i> Adamson | <i>Oxalis dentata</i> Jacq. |
| <i>C. hederifolia</i> (Burch.) Drude | <i>Polygala nematocaulis</i> Levyns |
| <i>C. triloba</i> (Thb.) Drude | <i>Phyllica buxifolia</i> L. |
| <i>Chondropetalum ebracteatum</i> (Kunth) Pillans | <i>P. dioica</i> L. |
| <i>C. nudum</i> Rottb. | <i>P. disticha</i> E. & Z. |
| <i>Cliffortia dentata</i> Willd. | <i>P. nigrita</i> Sond. |
| <i>C. glauca</i> Weim. | <i>Prismatocarpus nitidus</i> L'Her. |
| <i>C. intermedia</i> E. & Z. | <i>Restio bifidus</i> Thb. |
| <i>C. subsetacea</i> Diels ex Bolus & W.-Dod | <i>R. Dodii</i> Pillans |
| <i>Elegia cuspidata</i> Mast. | <i>R. Harveyi</i> Mast. |
| <i>E. squamosa</i> Mast. | <i>R. major</i> Pillans |

Hypolaena diffusa Mast.
H. digitata (Thb.) Pillans
H. laxiflora Nees
Juncus ananymus Steud.

R. multiflorus Spreng.
R. quadratus Mast.
Rorilla muscosa L.f.

The south-western component as a whole has been regarded by Weimarck and by Levyns as being the result of contraction of range as the result of an increased dryness of the climate. In other words, all the species in it are old and really relics. This is certainly supported by the high proportion of the component which exhibit discontinuity. A number of these discontinuous species are plants confined to the higher altitudes where the general drying of the climate would be least.

Wide. This is the largest of the components. As a whole it is not really uniform and can usefully be subdivided into a number of sections. The first of these contains those plants with a wide and continuous range. These are common plants that need no further comment. Many of them are also found in the flora of the Flats. Included here are:

Adenogramma Lichtensteiniana (Ser.) Druce
Agathosma capensis Link ex R. & S.
Centella affinis (E. & Z.) Adamson
C. glabrata L.
Cliffortia atrata Weim.
Dimorphotheca nudicaulis (L.) DC.
Elytropappus rhinocerotis (L.) Less.
Hypodiscus aristatus (Thb.) Nees
Metalasia muricata (L.) DC.
M. brevifolia (Lam.) Levyns
Muraltia alopecuroides (L.) DC.
M. pauciflora (Thb.) DC.

Pharnaceum elongatum (DC.) Adamson
P. dichotomum L.f.
P. lineare L.f.
Phyllaea eriophoris Berg.
P. imberbis Berg.
P. stipularis L.
Polypoda capensis Presl
Polygala bracteolata L.
P. garcini DC.
P. myrtifolia L.
Prismatocarpus fruticosus L'Her.
Restio cuspidatus Thb.

A second subgroup comprises those species with a wide but not continuous distribution. These are species that are undergoing contraction of range and as such old members of the flora. The contraction is less extreme than in the case of those in the south-western component.

Agathosma imbricata Willd.
Aristea glauca Klatt
Berzelia intermedia Schld.
Cliffortia polygonifolia L.f.
Elegia asperiflora (Nees) Kunth
E. coleura Nees
Elytropappus gnaphaloides Levyns

Juncus viridifolius Adamson
Leptocarpus distichus (Rottb.) Pillans
Lobostemon argenteus (Berg.) Beuk
Ornithogalum attenuatum Leighton
Osteospermum polygaloides L.
Stoebe plumosa (L.) Thb.
Restio Sieberi Kunth.

In some of these species the gaps in range are very wide.

Associated with the above-named are a number of species whose range approximates closely to the south-western component but has extensions to the north, the east, or both. Many of these exhibit some discontinuity.

**Agathosma bifida* Bart. & Wend.
Aristea africana (L.) Hoffm.
A. thyrsiflora (de la R.) N.E. Br.
Centella macrocarpa (Rich.) Adamson
Cliffortia eriocephala Cham.

Metalasia adunca Less.
Ornithogalum pilosum L.f.
Osteospermum spinosum L.
Oxalis multicaulis E. & Z.
Phyllaea callosa L.f.

- **C. intergerrima* Weim.
- C. ruscifolia* L.
- Disparago lasiocarpa* Cass.
- Elytropappus glandulosus* Less.
- E. scaber* (L.f.) Levyns
- **Hypolaena crinalis* (Mast.) Pillans
- **Leptocarpus vimineus* (Rottb.) Pillans
- Lightfootia subulata* L'Her.
- Lobostemon fruticosus* (L.) Beuk
- P. excelsa* Wendl.
- P. pubescens* Ait.
- **Restio filiformis* Poir.
- **Staberoha cernua* (L.) Dur. & Schinz
- **Stoebe aethiopica* L.
- **S. capitata* Berg.
- S. fusca* (L.) Thb.
- **Thamnochortus dichotomus* (Rottb.) R. Br.

Those species marked with an asterisk exhibit especially large discontinuities in their range. These plants are clearly in the same category as those in the southwestern component.

Another subgroup is composed of species with a range extending to the east but very little to the north. These are intermediate between the wide and eastern components.

- Aristea capitata* Ker
- Brunia nodiflora* L.
- Cannamois virgata* (Rottb.) Steud.
- Cliffortia strobilifera* Murr.
- Elegia parviflora* Kunth
- E. variegata* Mast.
- E. verticillaris* (L.f.) Kunth
- Gibbaria ilicifolia* (L.) Norl.
- Hypodiscus alboaristatus* (Nees) Mast.
- H. Willdenowianus* (Nees) Mast.
- Juncus lomatoxyllus* Spreng.
- J. oxycarpus* E. Mey.
- Lightfootia parvifolia* (Berg.) Adamson
- Lobostemon paniculatus* DC.
- Osteospermum truncatum* (L.) Norl.
- Oxalis incarnata* L.
- O. polyphylla* Jacq.
- O. stellata* E. & Z.
- Polygala refracta* Chodat
- Restio Gaudichaudianus* Kunth
- Staavia radiata* Dahl.

Finally there is a small group in which the range extends northwards but very little to the east.

- Berzelia lanuginosa* Brongn.
- Ornithogalum hispidum* Hornem.
- Osteospermum pulchrum* Norl.
- Oxalis glabra* L.
- Phyllica plumosa* L.
- Muraltia heisteria* (L.) DC.

General features of the components

The evidence obtained from a consideration of the geographical components points to the mountain flora as being ancient. The mountains on which this flora occurs are themselves a very ancient land surface which has persisted since Jurassic or Cretaceous times without essential change. During this long period there have undoubtedly been changes in climate though none appears to have been of sufficient magnitude to bring about a change in the kind of flora. The beginnings of the present flora must be traced back to these early times.

Climatic changes of a lesser kind have occurred and must be responsible for the restrictions in range of so many species that have obviously taken place. The main change seems to have been one towards a dryer climate which would have caused a retreat of the less tolerant species to the higher levels where the effects would be least. The extent to which such retreat has occurred points to a long period of rather slow change rather than to rapid fluctuations.

While this kind of retreat has been going on there has also been an appreciable amount of species differentiation. This is most clearly seen in the endemic species

that are regarded as relatively recent but can be shown to have occurred in many other cases. One example will suffice. The three species *Roella decurrens*, *R. squarrosa* and *R. amplexicaulis* are closely allied, and together form an endemic series in the genus which certainly seems to have arisen from a common ancestor. On the Peninsula there has been differentiation into these three species. *R. squarrosa* became differentiated on the northern part, on Table Mt., where it is abundant. As it is much less frequent on the mountains south to the Fish Hoek valley it may have spread there from Table Mt. In contrast *R. amplexicaulis* is frequent in the southern Peninsula and occasional between Fish Hoek and Constantia Nek. It evidently was differentiated in the south and spread northwards. The two species hybridize freely where they occur together.

Comparisons of the Peninsula flora with that of the adjacent mainland bring out great similarity and also some striking differences. Even with a sample as small as that investigated the differences are so marked that it appears that the area of the Flats must have been an appreciable barrier to free movement. The Peninsula flora presents many of the features of an off-shore island. From its position in relation to the mainland it might have been expected that its flora would exhibit some traces of a migration of species from north to south but as has been shown there is no support for this. The dispersal of species on the Peninsula and the large proportion with a limited range together with the presence in each portion of a number of peculiar species are all against any such migration. That it is the result of the population of detached areas, such as islands, fits much better.

SPECIES-GROUPS IN THE PENINSULA FLORA

Some of the points raised by consideration of the geographical components may be made clearer by examination of the distribution and habitat requirements of certain groups of species. A complete analysis along such lines has not been carried out but certain groups stand out.

Group A. These are species that are almost wholly confined to the highest levels where they exist in a relatively moist climate. The rainfall is higher and the dry period in summer mitigated by the prevalence of mists brought by the south or south-east winds. In this group are plants belonging to each of the geographical components. Among those in the wide component are: *Hypolaena crinalis*, *Juncus viridifolius* and *Restio Sieberi*. Of the eastern component are: *Aristea spiralis*, *Centella eriantha*, *Cliffortia odorata*, *C. ilicifolia*, *Juncus sphagnetorum*. Among the northern are: *Cliffortia Dregeana*, *Restio ochreateus*, *R. perplexus* and *R. tenuissimus*. Species in the south-western component are:

Centella caespitosa
C. flexuosa
C. hederacfolia
Chondropetalum nudum
C. Hookerianum
Hypolaena digitata
Leptocarpus gracilis
L. membranaceus

Ornithogalum Schlechterianum
Phyllaea dioica
P. strigosa
Prismatocarpus nitidus
Restio bifidus
Roella muscosa
Stoebe incana
Thamnochortus gracilis

Most of the species in this group exhibit some discontinuity in range. In some the gaps appear as the result of separation of possible habitats but in most they are much greater. The following examples will illustrate this. *Hypolaena crinalis* has a moderately wide distribution on the Hottentots Holland, Paarl-Wellington, Worcester and Swellendam mountains. *Phylica dioica* which occurs on most of the Peninsula summits is only known outside on the Stellenbosch mountains. *Prismatocarpus nitidus* occurs on the mainland as a variety recorded from the Wellington and Du Toit's Kloof mountains. *Restio tenuissimus* occurs on the southern part of the Hottentots Holland mountains, on the Paarl mountains and on the Cedarberg. *Restio sieberi* is recorded from Table Mountain and from mountains near Ceres.

These and other discontinuities can only be explained by a contraction of the original areas occupied and a disappearance of the species in the intervening parts. As the mountains on which the plants occur are part of an ancient and stable land surface that has existed without essential change at any rate since Cretaceous times, climatic change must have caused the restrictions. The plants all demand a cool moist climate and are not in full adjustment to the generally existing conditions. They appear to have become established under moister conditions than now exist.

As the one-time extent of these species was at least from the Cedarberg to the Langeberg, it would seem that the period of drying of climate that has resulted in the present discontinuous patterns must have been operating for a long time. Some support for this is got from a consideration of the associated endemic species.

Cliffortia Theodori-Friesii
Elegia intermedia
Leptocarpus ramosissimus
Phylica Schlechteri
Restio sarcocladus
R. pusillus

Roella squarrosa
Staberoha vaginata
Thamnochortus nutans
T. plumosus
T. sporadicus

With the single exception of *Cliffortia Theodori-Friesii* for which a local hybrid origin has been suggested, none appear as recent differentiations. They are rather isolated and ancient species.

Taking all these considerations together it would seem that this is a very ancient group, possibly among the most ancient in the flora. That the group is so numerous on the Peninsula may be attributed to the more oceanic climate and less severe drying.

Group B. This is a smaller group than Group A and like it dependent on rather moist conditions though less pronouncedly so. The plants here are not found at the highest altitudes. They occur on steep east-facing slopes, the base of cliffs, and at the margins of forests. They need some degree of increased moisture but distinctly less than those in Group A. In this group are:

Agathosma tabularis Sond.
Cliffortia intermedia E. & Z.
Elegia squamosa Mast.
Lobostemon montanus (DC.) Buek
Muraltia serpylloides DC.
Phylica buxifolia L.

Polygala myrtifolia L.
Restio Harveyi Mast.
R. multiflorus Spreng.
R. quadratus Mast.
Staberoha Banksii Pillans
Stoebe cinerea (L.) Thb.

Many of these species have some discontinuity in range. This group again appears as an old one but on account of its lesser habitat demands is probably less old than Group A. With it may be associated the following endemics:

Agathosma pulchella Link
Muraltia stipuacea (Burm.) DC.
M. curvipetala Levyns

Roella decurrens L'Her.
Thamnochortus Levynsiae Pillans

Group C. This is made up of plants restricted to the sides of permanent streams and to marshes. They are found at the higher levels on Table Mt. but many occur at much lower levels in the southern Peninsula where the mists brought by south-east winds affect even quite low levels. The distribution of these plants shows a close parallelism to that of the fresh-water Crustacea studied by Barnard (1927) and his conclusions that they are ancient but now restricted by limitation of habitat, are equally applicable. Many of the species in this group are more abundant on the mainland than on the Peninsula. The species here are:

Aristea juncifolia Baker
A. Zeyheri Baker
Cannamois virgata (Rottb.) Steud.
Chondropetalum mucronatum (Mast.) Pillans
Centella laevis Adamson
Elegia cuspidata Mast.
E. verticillaris (L.f.) Kunth
E. Neesii Mast.
E. thyrsoiflora Mast

Hypolaena diffusa Mast.
Polygala nematocaulis Levyns
Pseudobaeckia africana (Burm.) Pillans
Restio dispar Mast.
R. Dodii Pillans
R. compressus Rottb.
R. major Pillans
R. paludosus Pillans

Associated with this group are the endemics *Elegia fenestrata* Pillans and *Hypodiscus paludosus* Pillans.

Group D. This is composed of species all of which exhibit discontinuous or relic distribution. The plants are not, however, characteristic of the higher altitudes and do not at first sight show the clear relation to a changed climate that is seen in Group A. On the Peninsula a large porportion of this group are characteristic of the southern part. In this group are:

Agathosma ciliata Link
A. Hookeri Sond.
Aloe soccotrina Lam.
Audouinia capitata Brongn.
Chondropetalum Hookerianum (Mast.) Pillans
Cliffortia dentata Willd.
Disparago laxifolia DC.
Elytropappus longifolius (DC.) Levyns

Phyllica atrata Link.
P. nigrita Sond.
P. disticha E. & Z.
P. pubescens Ait.
Staavia Dregeana Presl
Restio bifurcus Nees
R. perplexus Kunth
R. quinquefarius Nees

This is certainly an old group as seen from the relic type of distribution. In some species the gaps in range are very large, e.g. *Agathosma ciliata* where the nearest station is Du Toit's Kloof, or *Restio quinquefarius* where it is the Cedarberg. With the group can be associated a number of endemic species that have the same features of habitat and which are largely found on the southern Peninsula. These are:

Agathosma lanceolata Link
Aristea rigidifolia Lewis
Lightfootia tenuis Adamson

Roella amplexicaulis W.-Dod
R. Goodiana Adamson
R. recurvata A.DC.

Muraltia brachypetala W.-Dod
M. diabolica Levyns
M. Pageae Levyns

R. triflora (Good) Adamson
Staavia Dodii Bolus
Stoebe rosea W.-Dod

Of these endemics *Muraltia brachypetala*, *Roella Goodiana* and possibly *R. amplexicaulis* seem relatively recent modifications.

The fact that so many of this group and of its associated endemics are found on or confined to the southern Peninsula seems explicable only by a study of the conditions in the past. This part is separated from the rest of the Peninsula by a low valley. The height of the lowest and most recent raised beach is such that this valley would have been submerged and the southern part would have been an island. The distinctness of the flora and the presence in it of locally differentiated species points to separation as having been long continued, even though the separation was not sufficient to prevent the passage of several characteristic species to the more northern parts.

At the present time the southern Peninsula does not attain any appreciable altitude, apart from the mountains near Simonstown, but it does have frequent mists even at sea level and hence has a climate moister than that of other parts for corresponding altitudes. Though the plants in this group are less dependent on moisture than are those of group A, they may well be survivors of an island flora which became established at a time when conditions were less dry.

General mountain flora. These groups which have been selected all appear as ancient parts of the flora. Together they represent, however, only a fraction of the total. The flora that occupies the drier mountain slopes has not so far been analysed in detail but there seems little doubt that much of it is less ancient than the selected groups and that there has been considerable species differentiation.

THE FLATS FLORA

Of the flora of the Flats a very large proportion also occurs on the mountains. Owing to the more recent nature of the habitat, the flora as a whole may be regarded as derived from the mountain flora. In the present discussion only those species which are characteristic of the Flats are considered. These are those occurring on the lower slopes. Species with a wide indifferent range and mountain species which occur sporadically on the Flats are not specially dealt with. In spite of these limitations a certain amount of duplication is unavoidable.

In the flora there are a few species which occur on the mountains on the mainland but not on those of the Peninsula. Among such are:

Aristea cuspidata Schinz
Cliffortia cuneata Ait.
Elegia grandis (Spreng.) Kunth
Lobostemon capitatus (L.) Buek
L. trichotomus (Thb.) DC.
Ornithogalum graminifolium Thb.

Oxalis bifida Thb.
O. minuta Thb.
Restio fruticosus Thb.
Stoebe bruniades Levyns
S. capitata Berg.

There are in addition a considerable number of plants on the Flats that do not occur on the mountains though some may be found on the lowest parts. Among these are a number that are found also on the level flats on the southern Peninsula.

The Flats present a much more uniform habitat than the mountains and less variety is to be expected. Included in the flora are a number of marsh or swamp plants and some definitely coastal in habitat. Some of the latter, such as the species of *Arthrocnemum*, are restricted to specialized habitats. Most of the flora, however, exists in a rather uniform habitat.

When the flora is divided into its geographical components the results are different from those reached in the mountain flora. The south-western component is much smaller and the eastern and northern relatively greater.

Endemic

Arthrocnemum capense Moss
Cliffortia hirta Burm. f.
C. obcordata L.f.
Elegia prominens Pillans
Hypertelis trachysperma Adamson
Juncus atropurpureus Adamson

Juncus filifolius Adamson
Restio micans Mast.
Tetragonia caesia Adamson
Storbe gomphrenoides Berg.
Willdenowia humilis Mast.

Most of these appear as relatively recent differentiations which have not spread from their position of origin. The exceptions are *Juncus atropurpureus* which is closely allied to *J. Sonderianus* Buchen., a species found only between Still Bay and Port Elizabeth. This type of distribution, which suggests an old species, is discussed under the eastern component. *Cliffortia obcordata* and *Willdenowia humilis* are both found also on mountains on the Peninsula and may have originated there. It is to be noted that Weimarck regards *C. obcordata* as not a very ancient modification.

Northern

Adenogramma Mollugo Reich. f.
Agathosma corymbosa G. Don
A. glabrata Bart. & Wendl.
Berzelia abrotanoides Brongn.
Chrysanthemoides incana (Burm.) Norl.
Cliffortia juniperina L.f.
 **Galenia crystallina* Fenzl var. *maritima* Adamson
Juncus inaequalis Buchen.
 **J. rupestris* Kunth
J. scabriusculus Kunth
 **J. stenopetalus* Adamson
 **J. umbellatus* Adamson
Lobostemon capitatus (L.) Beuk
L. paniculiformis DC.
Metalasia octoflora DC.
 **Muraltia brevicornu* DC.

M. dumosa (Poir.) DC.
M. macropetala Harv.
M. Thunbergii E. & Z.
M. thymifolia (Thb.) DC.
 **Mollugo pusilla* (Schltr.) Adamson
Osteospermum dentatum Burm. f.
Oxalis compressa L.f.
O. natans L.f.
O. tomentosa L.f.
Pharnaceum lanatum Bartl.
Phyllis cephalantha Sond.
P. Harveyi (Arn.) Pillans
P. strigosa Sond.
 **Tetragonia nigrescens* E. & Z.
Thamnochortus punctatus Pillans

Some of these species, marked by an asterisk *, exhibit large gaps in their distribution areas. These are discussed later.

Eastern component. Those species which show gaps in their distribution areas are marked by an asterisk *.

**Aristea pauciflora* W.-Dod
Arthrocnemum africanum Moss
 **A. perenne* var. *radicans* Moss
 **A. Pillansii* Moss

**Hypertelis arenicola* Sond.
Galenia herniariaefolia (Presl) Fenzl
Juncus capensis Thb.
 **J. effusus* L.

- **A. variiflorum* Moss
- Chondropetalum microcarpum* (Kunth) Pillans
- Cliffortia falcata* L.f.
- C. ferruginea* L.f.
- **C. graminea* L.f.
- C. stricta* Weim.
- Dimorphotheca fruticosa* (L.) DC.
- Disparago anomala* Schltr. ex Levyns
- Elegia fistulosa* Kunth
- J. punctorius* L.f.
- Lightfootia diffusa* Buek
- Muraltia ericoides* (Burm.) Steud.
- M. saturoides* DC.
- Phylica Dodii* N.E. Br.
- **Restio eleocharis* Nees
- R. tetragonus* Thb.
- **Roella compacta* Schltr.
- **Salicornia Meyeriana* Moss

It is noteworthy that a large proportion of these species exhibit gaps of varying extent in their distribution. In some cases the gaps may be the result of absence of specialized habitat conditions, as in the case of species of *Arthrocnemum*, but this does not apply to most of them. In some the gaps are as much as 100 miles. The explanation put forward by Levyns (1954) seems the most satisfactory, namely that there have been changes in sea-level in later Tertiary times which, though comparatively small, were sufficient to eliminate stretches of possible habitat. Quite large intervals may thus be the result of relatively recent changes in level. The gaps in general seem much less ancient than those which were noted in the mountain flora.

South-western. This component is relatively much smaller than that in the mountain flora.

- Adenogramma rigida* (Bartl.) Sond.
- **Chondropetalum nudum* Rottb.
- C. rectum* (Mast.) Pillans
- Cliffortia ericaefolia* L.f.
- C. cuneata* Ait.
- Elegia grandis* (Spreng.) Kunth
- E. Verreauxii* Mast.
- **Leptocarpus rigoratus* Mast.
- Lightfootia adpressa* (Thb.) A.DC.
- Metalasia imbricata* (Berg.) Harv.
- **Muraltia filiformis* (Thb.) DC.
- Muraltia mitior* (Berg.) Levyns
- M. saturoides* var. *floribunda* Levyns
- Oxalis minuta* Thb.
- O. pusilla* Jacq.
- Pharnaceum cordifolium* L.
- Restio bifurcus* Nees
- **R. major* Pillans
- R. paludosus* Pillans
- Roella prostrata* A.DC.
- Staberoha Banksii* Pillans
- Willdenowia sulcata* Mast.

In this component only a few of the species have discontinuous areas. Of those that have, *Leptocarpus rigoratus*, *Muraltia filiformis* and *Restio major* have gaps on the eastern coastal belt and come in the category that was mentioned under the eastern component. *Chondropetalum nudum* has stations at Saldanha Bay and on the mountains near Paarl and is probably an old mountain plant that has spread to the Flats. For the rest the range is between False Bay in the south and Saldanha Bay in the north. Some extend over the whole area, some are much more restricted. These species appear to be relatively recent developments which have not spread much beyond their place of origin and so form a modern part of the flora.

Wide. This component is larger and can conveniently be divided into those with a continuous range and those which exhibit distinct gaps. In the first are:

- Agathosma serpyllacea* Link ex. R. & S.
- Centella coriacea* Nannfd.
- C. tridentata* (L.f.) Drude
- Chrysanthemoides monilifera* (L.) Norl.
- Cliffortia polygonifolia* L.f.
- Galenia africana* L.
- Oxalis depressa* E. & Z.
- O. Eckloniana* Presl
- O. flava* L.
- O. pes-caprae* L.
- O. purpurea* Thb.
- Polygala affinis* DC.

<i>G. pubescens</i> (E. & Z.) Druce	<i>Phyllica parviflora</i> Berg.
<i>G. secunda</i> (L.f.) Sond.	<i>Restio fruticosus</i> Thb.
<i>Juncus bufonius</i> L.	<i>Roella ciliata</i> L.
<i>J. cephalotes</i> Thb.	<i>Stoebe plumosa</i> (L.) Thb.
<i>J. Kraussii</i> Hochst.	<i>Tetragonia decumbens</i> Mill.
<i>Muraltia ericoides</i> (Burm.) Steud	<i>T. herbacea</i> L.
<i>Ornithogalum thyrsoides</i> Jacq.	<i>T. microptera</i> Fenzl
<i>Osteospermum clandestinum</i> (Less.) Norl.	<i>T. portulacoides</i> Fenzl
<i>Oxalis corniculata</i> L.	<i>T. spicata</i> L.f.

In the group with discontinuities are:

<i>Aristea cuspidata</i> Schinz	<i>Elegia stipularis</i> Mast.
<i>Arthrocnemum littoreum</i> Moss	<i>Juncus Dregeanus</i> Kunth
<i>Centella capensis</i> (L.) Domin	<i>Staberoha distachya</i> (Rottb.) Kunth
<i>Chondropetalum tectorum</i> (L.f.) Pillans	<i>Thamnochortus erectus</i> (Thb.) Mast.
<i>Cliffortia ramosissima</i> Schltr.	<i>T. fruticosus</i> Berg.
<i>C. strobilifera</i> Murr.	<i>T. spicigerus</i> (Thb.) R. Br.
<i>Dimorphotheca pluvialis</i> (L.) Moench.)	<i>Willdenowia teres</i> Thb.
<i>Elegia coleura</i> Nees.	

This component needs little comment. It contains a number of coastal plants and of marsh plants. Of the discontinuous species some are certainly old mountain plants which have spread on to the Flats, others come under the category considered above.

General considerations

From a consideration of these geographical components the conclusion is reached that the flora here is much less ancient than that of the mountains. As it contains such a large proportion of species also in the mountain flora, it must be the case that these have spread to the Flats from their older stations. It is worthy of note that in some cases species which have a discontinuous range on the mountains are found on the Flats.

There are in addition to these mountain species a number which are confined to the coastal plains. Some of these are certainly derivatives from mountain species but others have a less certain origin. Of the species restricted to the plains, quite a considerable proportion have a rather limited range on the Cape Flats and appear as species which have not yet had time to spread widely. These must be recent. Those with a wide range over the coastal plains appear older. As many of these show discontinuities especially along the south coast, it is necessary to consider some aspects of the history of the region to discover their possible period of origin. As noted earlier the present extent of the coastal plain has not been constant. Elevation or depression of the land of quite small extent would greatly alter the possible habitats. Within the later Tertiary epoch it is known that such fluctuations have taken place. The frequency of gaps in range to the east of the Peninsula indicate submergences of the habitat. Some of these submergences must have taken place sufficiently long ago to permit differentiation of the surviving relics. For example *Juncus atropurpureus* on the Cape Flats and *J. Sonderianus* on the coastal plain near Port Elizabeth are clearly derived from a common ancestor. Indeed, Weimarck (1946) is of opinion

that they are conspecific. Even though a considerable period of time is necessary, this seems to have been less than that during which the regression of so many of the mountain species has been under way.

On the western coastal strip the same considerations can be applied though here the increasing aridity north of the Peninsula is also a factor. On this strip there are some species that are more characteristic of drier conditions further north and which reach the limit of their range on the Cape Flats. Among these are:

<i>Adenogramma Mollugo</i> Reichb.	<i>Mollugo pusilla</i> (Schltr.) Adamson
<i>Centella capensis</i> (L.) Domin	<i>Osteospermum clandestinum</i> (Less.) Norl.
<i>Galenia crystallina</i> var. <i>maritima</i> Adamson	<i>Pharnaceum lanatum</i> Bartl.
<i>G. africana</i> L.	<i>Tetragonia nigrescens</i> E. & Z.
<i>Juncus stenopetalus</i> Adamson	

When such species are considered along with a number of others not included in the sample, which reach their southern limit on the drier parts of the Peninsula, it seems possible that there was a migration southwards during a climatically drier phase.

A number of species in the flora of the Cape Flats extend on to the lower slopes of the mountains. Some of these seem at present to be in course of extension and invasion. Examples out of many are seen in:

<i>Chrysanthemoides monilifera</i> (L.) Norl.	<i>Muraltia heisteria</i> (L.) DC.
<i>Cliffortia polygonifolia</i> L.f.	<i>Roella ciliata</i> L.
<i>Dimorphotheca pluvialis</i> (L.) Moench.	

Such examples, which could be much extended, again point to the Flats flora as the younger one.

GENERAL SUMMARY AND CONCLUSIONS

A preliminary phytogeographical analysis of a sample of the flora of the Cape Peninsula has been carried out.

The species have been grouped in geographical components based on the range on the mainland in relation to the Peninsula. These are endemic, northern, eastern, south-western and wide.

On the Peninsula itself the distribution shows no centre of concentration nor is there any evidence for any mass migration along its length. There is a high proportion of species with limited range.

The flora is divided into two parts, that of the mountains and that of the flats. The mountain flora is the larger and is shown to be very ancient. Much of it has become restricted in range probably on account of a drying of the climate. Part of the flora is today confined to stations where especially moist climatic conditions are available.

The Flats flora is more recent. Much of it is derived directly from that of the mountains but a part is found only on the coastal plains. While many of its constituents seem recent developments that have not spread from their origination on the Flats, others are widespread and a considerable number have discontinuities

especially along the south coast. These discontinuities are shown to be the result of changes in habitat much more recent than those that have brought about the restrictions in range of the mountain plants.

The conclusions agree entirely with the views expressed by Levyns and by Weimarck.

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THE ECOLOGY OF SOUTH AFRICAN ESTUARIES
PART IX: NOTES ON THE ESTUARY OF THE ORANGE RIVER

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(With two text-figures)

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The Orange River presents a type of estuary previously undescribed for southern Africa. The estuarine fauna is extremely poor and lacks a true estuarine component. An analysis of the physical and chemical conditions indicates that the environment is particularly forbidding and it is suggested that the striking paucity of the fauna may be related to the short length of the estuary in winter and its complete disappearance in summer.

INTRODUCTION

With one exception the estuaries so far considered in this series of papers have been the estuaries of rivers flowing into the Indian Ocean. These east coast estuaries have been shown to be fairly well defined and in general to harbour a rich fauna. Milnerton estuary is the only west coast estuary which has been described (Millard and Scott, 1953) and the evidence would suggest that this is by no means a typical west coast estuary. Three large estuaries lying further north have now been investigated: the estuaries of the Berg, Olifants and Orange Rivers. The fauna of the first two estuaries is extremely poor when compared with east coast estuaries, and there is an almost complete absence of estuarine animals in the Orange River. As no such estuary has previously been described from southern Africa, it is proposed to deal here only with that of the Orange River and to publish an account of the Berg and Olifants River estuaries at a later date.

The present report is the product of an expedition to the Orange River mouth by a party from the Zoology Department, University of Cape Town, consisting of Messrs. D. E. van Dijk, B. M. H. Bush, J. R. Grindley and the author. The period 5th to 10th July, 1956, was spent investigating the chemical and physical conditions and the macroscopic fauna of the mouth, particularly of the intertidal region of the south bank. The north bank was unfortunately not accessible to the party, as it forms part of a diamondiferous area. In addition to the work undertaken by the party, some useful information has been obtained from reliable local sources and Mr. R. Liversidge, of the Port Elizabeth Museum, has contributed to our knowledge with his notes on the condition of the estuary in summer.

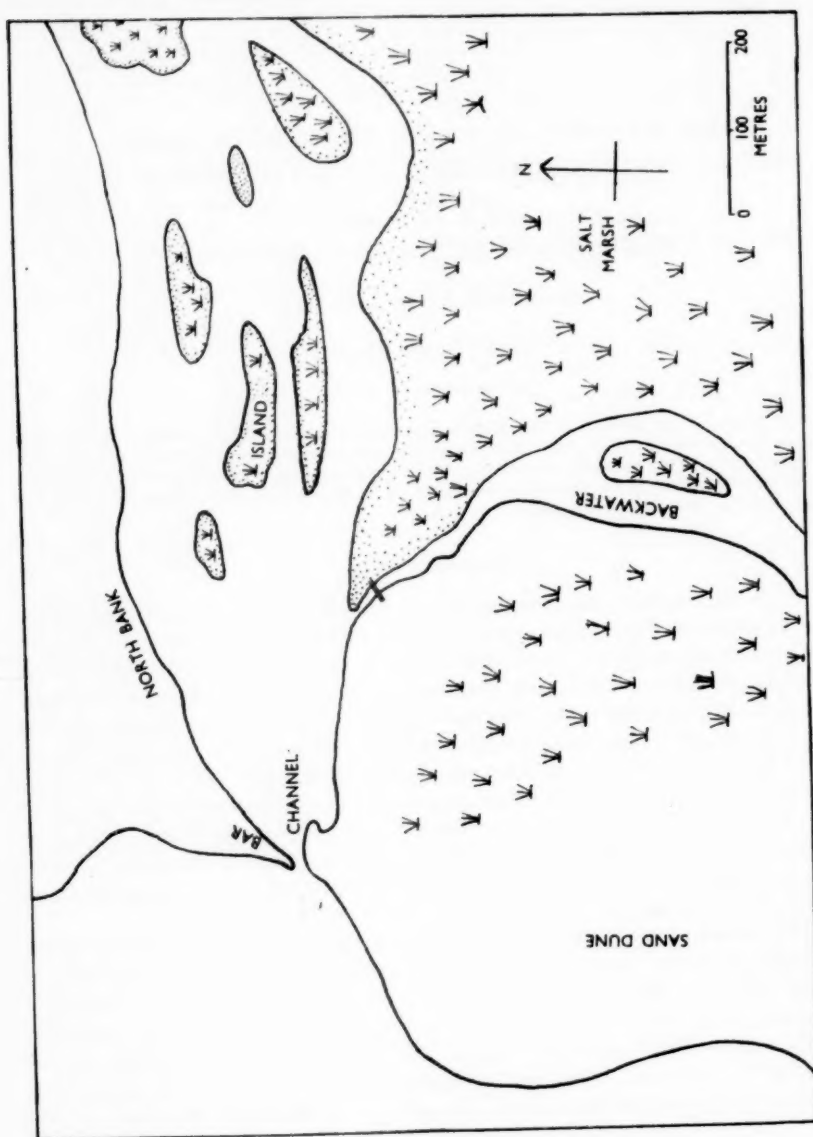


FIG. 1. Map of Estuary.

The field-work involved in this survey has been considerably less than that on which previous papers in the series have been based. It has nevertheless been decided to publish an account of the estuary at this stage in view of the fact that a second expedition to the area will not be possible in the near future. The data collected are sufficient to show the Orange River estuary to be of a new and interesting type, the most remarkable feature of which is the paucity of the fauna.

Though the almost complete absence of estuarine flora and fauna will be our main concern, the chemical and physical conditions of the estuary will be described first, thus continuing the practice so far adopted in this series of publications.

TOPOGRAPHY

The lower reaches of the Orange River form the natural boundary between the Cape Province and South West Africa. The system of rivers which unite to give rise to this water-way is by far the largest in the entire Union of South Africa. The area drained is vast and includes almost the whole of the Orange Free State, most of the Transvaal, and parts of the Cape Province, Basutoland, Bechuanaland and South West Africa. The whole of this area falls within the summer rainfall region, winter rains being uncommon. While summer rains in the inland catchment areas are often heavy, precipitation near the coast seldom occurs, the region being semi-desert. In the coastal region temperatures are relatively low, humidity is high, and morning mists often persist until noon. Such conditions are common along the whole of the west coast and as far as the intertidal fauna is concerned represent decreased exposure to desiccation.

As appears to be usual during the dry season, a sand bar was present at the mouth when the party visited it. This was broken close to the south bank, leaving a channel some 30 metres wide. On the seaward side of the channel the sea-shore was parallel to the bar and steep and sandy. The shore was less steep at the mouth of the channel; just behind the bar the slope was gradual to the water's edge, where there was a vertical drop to the water of approximately one metre. Similar conditions could be seen on the north side.

Within the bar the slope was at first steeper than in the channel, then decreased as the shore curved away from the bar to form the bank of the first of a series of tidal backwaters communicating with extensive salt-marshes. These salt-marshes were separated from the sea-shore by a large sand dune, increasing in width from approximately 100 metres at the mouth. There was a large amount of drift-wood on this sand dune, reaching to 12 metres above low water of springs level, and indicating that much of the area, including the salt-marshes which are over $3\frac{1}{2}$ miles wide, must at times be inundated by flood-waters. This opinion was confirmed by local inhabitants.

The first of the backwaters, already referred to, marked a boundary between sand, extending down towards the mouth of the estuary, and extremely fine mud, extending up the river for at least 5 miles (the extent of our investigation). There appeared to be no transition zone between sand and mud.

The estuary itself is very shallow, reaching a depth of a little over 2 metres in only a few places when the mouth is open in winter. The drift-line on the sand dune indicates, however, that it may be as deep as 14 metres during floods.

MOVEMENTS OF WATER

The surface current velocity was measured at the inner limit of the sand bar in approximately mid-channel. The greatest velocity recorded was 0.78 metres/second, measured at the time of low water of springs in the sea. The tide at this inner limit of the bar was 1 hour and 30 minutes behind that of the sea, there being no surface current at this time. That a great deal of suspended matter is carried by the river even when current velocities are low is evident from the fact that a Secchi disc, placed in the water at the turn of the tide (H.W.S., when one might expect suspended matter to be near its minimum value) could no longer be seen at a depth of 25 cm. below the surface of the water.

The tidal lag was also measured at a crude bridge constructed across the first backwater, some 2.5 metres from its junction with the main body of the estuary. The low-water lag here was 3 hours 20 minutes, while the high-water lag was 1 hour 10 minutes. Both values refer to spring tides.

TEMPERATURES

Temperatures were recorded on 7th and 8th July. On the first date, one day before spring tides and with low water occurring at 8.40 a.m., the temperature of the sea immediately outside the mouth was noted at 10 a.m., noon, 2 p.m. and 3 p.m. On each occasion the temperature was 14°C. At 10.05 a.m. the temperature within the estuary, just behind the bar, was 15.0°C., and at noon 15.25°C., while at the bridge over the backwater the temperature was 15.5°C. at 10.30 a.m. and 16.5°C. at 3.15 p.m. (After the early morning mists had dispersed the day was bright and sunny.)

On 8/7/56, L.W.S. occurring at 9.22 a.m., the mist did not rise until 11 a.m. The sea temperature at 10.15 a.m. and at 11.0 a.m. was 13.75°C., while the temperature at the inner limit of the bar was 15.0°C. at noon.

The available records indicate that there is a marked difference between winter and summer temperatures in the river but that the temperature of the sea is not appreciably higher in summer than in winter. In summer the temperature of the river often rises above 25°C. The average maximum temperature of the river near Alexander Bay, between 20th and 25th January, 1958, was 24.0°C. This water flows into saline water whose temperature is 14°C. or less.

THE MUD SUBSTRATUM

The mud forming the substratum above the first backwater on the south bank was of such fine particle size as to appear non-porous when submerged pieces were removed and broken open. Furthermore the anaerobic black layer was found to

extend to within a centimetre of the surface, the smell of H_2S being noticeable whenever the mud was disturbed in any way.

A sample of mud from low-water mark, immediately behind the bridge, was removed and later analysed in the laboratory, following in general the methods outlined by Morgans (1956). The results of this analysis are shown in Table I where $Md\phi$ represents a reciprocal factor of the average particle size and $QD\phi$ a function

TABLE I. SUBSTRATUM ANALYSIS

Sample	% weight of particles retained by standard sieves meshes per inch							% available organic content	$Md\phi$	$QD\phi$
	6	12	25	52	100	200	Sub-sieve			
MUD South Bank L.W.S.	—	—	—	—	0.5	25.4	74.1	1.2	3.98	0.60
SAND Mouth L.W.S.	—	0.6	59.0	39.0	1.4	—	—	0.0	0.54	1.16
TRANSECT SAND Above L.W.S.	—	—	6.4	76.2	16.5	0.7	0.2	0.06	1.55	0.81
Upper intertidal	—	—	8.1	60.6	30.8	0.4	0.1	0.0	1.64	0.92
L.W.S.	—	8.6	72.9	16.5	1.3	0.4	0.2	0.0	0.15	0.79

of the degree of sorting. It will be seen from the table that the average particle size of the mud was very small, 74.1 per cent of the particles passing through even the finest of mechanical sieves. The organic content was high.

THE SAND SUBSTRATUM

Sand was collected from the mouth of the estuary and later analysed. The results, also recorded in Table 1, present a marked contrast with those obtained for the mud substratum. In addition to the particle size being larger, with no sub-sieve particles, there was no measurable organic content present.

EROSION

It is unfortunate that no measurements of erosion could be made in the short time available. However, certain observations that were made are worth recording. Wave-action in the mouth was on all occasions very strong. The waves were at least 2.5 metres high and were so violent that data could not be obtained by the usual methods.

In the mouth of the estuary erosion is very great. On 8/7/56 at high tide, large quantities of sand could be seen being swept away from the north side of the channel

and at the transect site, within the bar, stakes pushed 30 cm. into the sand in the intertidal zone and left overnight had been eroded away even from H.W.S. level by the next morning.

That these strong currents decrease rapidly away from the mouth is indicated by the fact that the footprints of birds, noted near the water's edge just above the tidal backwater on 8/7/56 were still visible on 9/7/56. It must, however, be remembered that firm compact mud is far less liable to erosion than is beach sand.

SALINITY

The few readings of salinity which were taken indicate widely fluctuating conditions, as shown in Table 2. At the time of low water of springs in the sea, the fresh river-water extended down through the channel and there was little dilution by sea-water even immediately outside the mouth. At high water of springs tide, however, the opposite picture was presented. Sea-water of high salinity then pushed its way up the channel to beyond the limit of the sand bar. Moreover, the surface and bottom salinities were almost identical at this time, indicating vertical homogeneity.

TABLE II. SALINITIES

Sample	Tide	Date	Salinity in parts per thousand
At the bar	L.W.S.	8/7/56	4.51
Outside mouth	L.W.S.	8/7/56	6.29
Bottom within bar	H.W.S.	9/7/56	34.74
Surface within bar	H.W.S.	9/7/56	34.79

These conditions do not persist all the year round. Aerial photographs are available which show the sand bar completely closing the mouth of the estuary. Local inhabitants state that this is of frequent occurrence during the dry season and that under such conditions the Alexander Bay drinking-water, which is piped from the river some $5\frac{1}{2}$ miles above the mouth, becomes so saline as to make the reopening of the bar by artificial means necessary. Local inhabitants also agree that on some occasions the development of a sand bar cuts off fresh water from the sea, the water even immediately behind the bar being then of drinkable quality even when the mouth has been closed for some months.

Mr. Richard Liversidge visited the Orange River mouth in January 1958 and has been able to supply a useful account of the conditions prevailing in mid-summer. The sand bar had disappeared and the river was in full flood. There was no indication of salinity changes within the bar and it appeared from the discoloration of the sea-water that the fresh water from the river extended for some miles out to sea. There was little apparent check to the current even at the time of high water of springs. Pump stations 20 yards from the original bank had been washed away and completely new channels had been cut in the river-bed. Mr. Liversidge describes the state of the river-water as 'liquid mud'.

A TRANSECT IN THE INTERTIDAL ZONE

To return to the winter picture; a transect was established across the intertidal sands just within the mouth, at the time of low water of springs on 8/7/56. A number of stakes were driven into the sand in a line at right angles to the water's edge, the first being established above H.W.S. level and the last 20 cm. below L.W.S. Sand was collected from the vicinity of each of these stakes for laboratory analysis and temperature readings were taken. The depth of the water-table was also noted, where possible, in holes previously dug in the transect line. The result of sand analysis are given in Table I, while the transect as a whole, including the shore profile, temperatures and animals collected, is shown graphically in fig. 2.

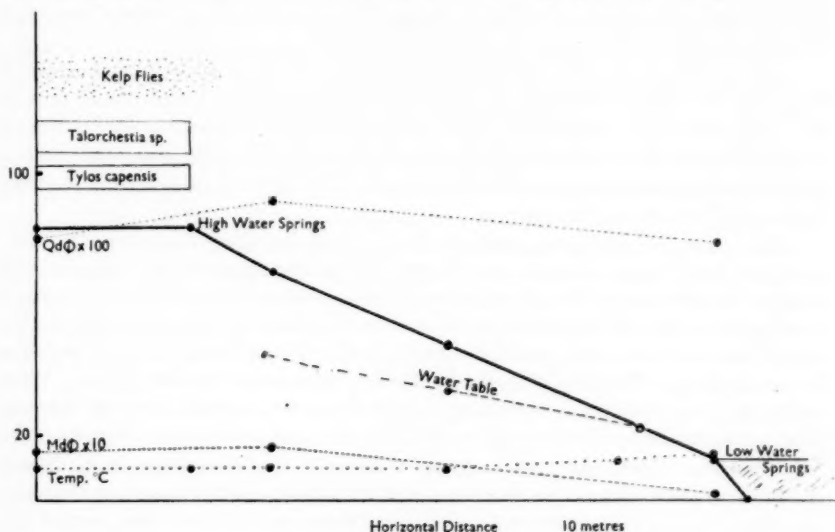


FIG. 2. Transect within the Bar.

The horizontal co-ordinates refer specifically to distances in metres. The vertical scale is unspecific and is contrived in such a way that the values of $Qd\phi$, $Md\phi$ and temperatures in degrees centigrade, as well as the slope of the beach and the depth of the water-table in centimetres, may be read from it.

It will be seen that the sand in the upper part of the transect was somewhat finer than that collected from the mouth itself, whereas in the lower part of the transect the sand was very coarse indeed, consisting mostly of water-worn pebbles. This is by no means an unusual phenomenon and is explained by the fact that this part of any foreshore is subjected to maximum turbulence and is never free from the action of water currents. Under these conditions large particles only are deposited.

When the transect-site was visited the following morning the entire area had completely altered overnight. The stakes had been washed away and the profiles were strikingly different to the eye, the slope being a great deal steeper.

THE FLORA AND FAUNA OF THE ESTAURY

The remarkable paucity of animals and plants in the waters of the estuary has been mentioned in the introduction. The above account of the chemical and physical data collected gives some idea of the conditions accounting for this paucity. It now remains to discuss the few organisms found within the estuary.

In the entire stretch of mud substratum investigated; that is from approximately 5 miles upstream to the beginning of the sandy zone within the bar, no organisms were found. Large quantities of mud were put through fine sieves—a difficult procedure due to its clay-like structure—without result.

Sifting sand through a sieve of larger mesh, throughout the length of the sandy region, both from near and below the water, also produced no animals of any kind, though over eight hours were spent in this manner.

Above tide-marks, four species were found to be present. The commonest of these was the Talitrid Amphipod *Talorchestia quadrispinosa* Barnard, found only in the sandy zone but apparently more or less evenly distributed along its length, round the sand dune and back along the sandy sea-shore. The maximum density recorded was 54 specimens per square metre, obtained by digging and on the surface, at the top stake of the transect.

The sand Isopod, *Tylos granulatus* Krauss, was found to be present in some numbers, being most common on the top of the sand dune separating the salt-marshes from the sea. The distribution of these animals over the sandy area was clearly due to their habit of starting to burrow in depressions already present in the sand. Burrows were common in footprints, and a line of burrows was found in a furrow made by dragging a spade lightly over the sand the day before. What appeared to be one burrow often proved to be the point of entry of several animals. They are essentially nocturnal and were found on the surface of the sand only at night.

The third supra-tidal species recorded was the kelp-fly *Lamproscatella dichæta* (L.W.), present but by no means common at the mouth. Kelp was present in small quantities only on the seaward side of the sand dune and fly larvae and pupae were found beneath this.

The fourth species was the only living animal other than birds recorded from the mud at the fringe of the salt-marshes; a Staphylinid beetle of the genus *Philonthus*. It was common in isolated patches.

Plankton-netting in the estuary met with little success. Netting at the bar, on an incoming tide, produced a single specimen of *Eurydice longicornis* (Studer) after an hour's work, and netting on an outgoing tide produced a juvenile specimen of the fish *Mugil cephalus* Linn., one beetle larva and two Copepoda. Netting in the back-water gave a somewhat larger catch, consisting of nine specimens of the Isopod *Eurydice longicornis*, seventeen Copepoda and a Dytiscid beetle.

Several hours of seining in the channel produced one individual of *Liza ramada* (juvenile) and one *Mugil cephalus*.

These were the only animals, apart from birds, encountered during the five days spent at the estuary.

Though it is not intended to give here an account of the birds of the estuary, it is interesting to note the presence in some numbers of both the Lesser and Greater Flamingoes, *Phoeniconias minor* (Goeffr.) and *Phoenicopterus ruber roseus* (Pall.). The Avocet, *Recurvirostra avosetta* (L.), was in evidence, as was the African Shelduck, *Tadorna cana* (Gmel.) and the Egyptian Goose, *Alopochen aegyptiaca* (L.). The only true ducks seen were *Anas capensis* (Gmel.) and *Anas erythrorhyncha* (Gmel.). None of these were seen to feed in the estuary itself.

Land animals were not collected from the salt-marshes as this was felt to lie outside the scope of an estuarine survey. The common plants of the marshes were, however, identified. *Arthrocnemum perenne* was found to dominate that part of the marsh nearest the water but this soon gave way to *Arthrocnemum africanum*, which proved to be by far the commonest plant present. *Salicornia meyeriana* and *Arthrocnemum australasicum* occurred in isolated patches.

DISCUSSION AND CONCLUSIONS

The most striking feature of the Orange River estuary is the paucity of its fauna. This is particularly so as studies of other South African estuaries have shown how very abundant the fauna of an estuary can be. Knysna estuary (Day, Millard and Harrison, 1952) provides an outstanding example of an estuary rich both in numbers and in species. It is interesting to note that in almost every aspect of the physical environment the estuaries of Knysna and the Orange River provide a marked contrast. The Orange River drains a vast area, the Knysna river a comparatively very small one; in the Knysna estuary the flow of water and the level of the water is not markedly different between summer and winter, while the Orange River shows immense seasonal changes and floods large areas of the surrounding country after heavy summer rains up country. Even with the small flow of water in winter, the Orange River carries a large quantity of suspended matter and its condition in summer has been described as liquid mud, again Knysna estuary presents a contrast—'it is probable that the clarity of the Knysna water is largely responsible for the luxuriance of the submerged vegetation and the richness of the fauna' (Day *et al.*, 1952). Furthermore, only two types of substratum are available for colonization in the Orange River estuary—very coarse sand with a negligible organic content, which is almost constantly being moved by the currents, and extremely fine mud of clay-like consistency, of high organic content but deficient in oxygen. Knysna estuary, on the other hand offers a variety of habitats, none of which are comparable with the two extremes described for the Orange River; and these habitats include rock and attached plants, both of which are stabilizing influences and both of which are absent from the Orange River estuary.

Although the sea is colder on the west coast than on the south coast, there is little difference in the temperatures of the river-water in the two areas. Thus animals living in the Knysna estuary will be subjected to less marked changes in temperature than will the fauna of west coast estuaries. While this may account in part for the paucity of the fauna of the Berg River and Olifants River estuaries, it cannot account

for the complete lack of estuarine species in the Orange River as the temperature variations are generally not large enough and are at times completely absent.

The survey of Milnerton estuary has already been mentioned, and some comparison may be appropriate here between this and the Orange River estuary as both occur on the South African west coast. It may be stated at once that temperatures and temperature differences between the river-water and the sea are comparable for both these estuaries. Another factor which these two estuaries have in common is the high turbidity to be encountered even when the flow of water is slight. At Milnerton 'the river-water is laden with silt, and plant growth is limited by continual deposition of mud and by poor light penetration. . . . The estuary thus lacks one of the richest habitats of other estuaries' (Millard and Scott, 1953). The authors assert that the fauna of Milnerton estuary is strikingly poor; this is a purely relative statement, based on comparison with south and east coast estuaries. The paucity of life in the Milnerton estuary does not approach that of the Orange River.

There are several major differences between these two estuaries; Milnerton lies in the winter-rainfall area and receives the run-off from a very small region of the western Cape Province while the Orange River drains a vast area, all of which lies in the summer-rainfall region. Unlike the Orange River, Milnerton is not subjected to extensive flooding and its lower reaches are saline throughout the year.

The opinion of the author, based on the evidence available, is that the paucity of the fauna and the complete absence of an estuarine component may be explained by the fact that for long periods of time the Orange River possesses no true estuary. An estuary may be defined as that part of a river 'where there is an appreciable variation in salinity due to the sea' (Day, 1951). Animals living in an estuary so defined are capable either of withstanding this variation or of moving up and down the estuary so as to avoid it, or they live in burrows or buried in the substratum where salinity variations are less apparent. The Orange River presents such estuarine conditions in winter but the estuary is significantly short and at low tide the fresh water extends down to and beyond the mouth. An animal living in the area described would have to contend not only with changes in salinity which might be defined as 'variation', but with changes from fresh water to actual sea-water. Moreover, rains decrease the extent of the estuary and the greatly increased flow characteristic of summer eliminates it altogether.

It is significant that not a single species recorded was restricted to the area under discussion; all were found also on the sea-shore or in the fresh water of the river, and the impression gained was of sampling the last outposts of two distinct eco-systems, neither fauna being concentrated in the area but present by accident and represented by only a few individuals.

On the above considerations it is clear that the Orange River estuary provides a far harsher environment than any other South African estuary so far investigated.

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in this survey and is also indebted to Professor J. H. Day for making the expedition possible, as well as for his advice and encouragement. Expenses were met by a grant from the Council for Scientific and Industrial Research. He also wishes to thank the National Diamonds Area Corporation for allowing the field-work to be carried out on their property and for making our stay a pleasant one. Mr. G. Malan, formerly of Alexander Bay, supplied much useful information and we are indebted to Mr. U. Keyser, of Kleinmondstrand, for summer temperature records, as well as to Mr. R. Liversidge, of the Port Elizabeth Museum, for his description of the Orange River estuary in flood.

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THE BIOLOGY OF LANGEBAAN LAGOON: A STUDY OF THE EFFECT OF SHELTER FROM WAVE ACTION

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(With seven text-figures)

(Read June 18, 1958)

The physical characteristics of the Saldanha Bay-Langebaan Lagoon system are described and it is shown that there are graded changes in wave action, substratum, temperature and salinity between the bay and the head of the lagoon. None the less the lagoon is not an estuary but a sheltered inlet of the sea.

Two transects of rocky shores and four transects of sandy shores are described and these are then used to illustrate the effects of increasing shelter on physical factors of the environment and the vertical zonation of the fauna. On sandy shores it is shown that zonation is more closely related to the depth of the water-table than to tidal levels.

An annotated list of species is given in the appendix which shows changes in species and their relative abundance throughout the system. This list is analysed to determine the changes in faunistic composition which occur with increasing shelter. On rocky shores there is an impoverishment of the fauna but no essential change in composition. On sandy shores there is an enrichment of the fauna and significant changes in composition. One part of the sheltered water fauna is derived from exposed rocky shores, another part is restricted to sheltered waters and a third is derived from species which elsewhere occur only below tide marks. The whole fauna of a sheltered inlet is very similar to that of the middle and lower reaches of an estuary. It is concluded that most so-called estuarine species are merely calm-water species.

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INTRODUCTION

The aims and objects of the present work are best explained by reference to a recent paper on Durban Bay by Day and Morgans (1957). In this paper an attempt was made to investigate the ecology of a sheltered bay and to determine the origin, composition and distribution of its fauna. In particular, comparisons were made

between the conditions of life and fauna of an exposed shore, a sheltered bay and neighbouring estuaries. The conclusions that could be drawn from these comparisons were limited by the fact that Durban Bay is no longer a natural environment but a busy port with concrete piers, dredged channels and polluted backwaters. Moreover, little is known of the sub-tropical dredged fauna of the Natal seas. As a result the discussion had to be limited to the shore fauna and the conclusions were guarded.

In brief, the aim of the present paper is to check and extend the tentative conclusions obtained earlier, by the study of a completely unspoilt area with an entirely different fauna. Langebaan Lagoon which opens into Saldanha Bay on the Atlantic coast of South Africa is ideal for this purpose. There is no pollution and no harbour development. There is a convenient series of collecting stations showing a progressive reduction in wave action on both rocky and sandy shores; the shore fauna is well known and even the dredged fauna has been explored to a certain extent. Most important of all, Langebaan is only 100 miles (161 km.) from the University of Cape Town and has been used for the past ten years as a training ground for students of marine biology. Some thirty students plus staff visit the area every year during the Easter vacation, and it is to these parties that I owe the enormous amount of material upon which the distribution lists in the appendix are based. They also helped to survey the transects, made records of temperature and tidal data and collected samples for salinity and substratum analysis. Without their help the work could never have been done; if there are errors they are mine for I directed the work.

Although Langebaan is well known as a good collecting ground only a few papers on its ecology have been published. Korringa (1956) has discussed the problem of sub-fossil oysters in the lagoon and gives some data regarding hydrological conditions. Odd records of temperatures and salinities also appear in the reports of the Division of Fisheries and these have been incorporated with our own more extensive data in the relevant section. At the same time I wish to acknowledge my thanks to the Division for doing some of the salinity titrations. Professor W. E. Isaac (1956) and his colleagues of the Botany Department made a survey of *Gracilaria confervoides* which is an important source of agar. I also wish to thank Miss J. Graves of the same department for identifying many of the algae whose names appear in the appendix. I have not discussed the birds of the lagoon for their ecology has recently been described by my colleagues Thesen, Liversidge and Broekhuysen (1958).

METHODS

The methods used were well-tried ones, but for the sake of convenience they are briefly set out below.

Collections were made by hand on rocky shores, digging and sieving on sandbanks, hand-netting in weed-beds and the use of the Saltash tuck-seine at night in the deeper channels. A 24-inch rock-dredge was worked in various parts of the lagoon, the channel and Saldanha Bay down to a depth of 10 fathoms (18 metres). Both coarse and fine plankton nets were fished in various areas, mainly at night, but it

may be noted that this paper deals mainly with the benthonic fauna and the plankton will be described separately.

None of the above collections were intended to be quantitative; nevertheless as individual samples were collected and sorted, notes were made of the relative abundance of each species using the categories described on p. 503. The symbols in the appendix thus show the changing density of each species from place to place.

Transects: Quantitative collections of the beach fauna were made at intervals along a number of surveyed transects. The survey work was done very simply with two surveyor's ranging poles marked in feet and using the sea horizon as a levelling device. The horizontal distance between any two points A and B on a transect is first measured with a surveyor's tape. One observer stationed at A then holds his eye level with some convenient mark (say 5 feet; 1.5 metres) on his own pole and looks past B to the horizon. He then signals to the second observer holding the pole at B to move a cardboard slide up or down the pole until the 5-foot mark on A, the slide on B and the horizon are all in line. The vertical distance between the slide and the 5-foot mark on pole B will then show the rise or fall between the two points. So long as the horizon distance is 2 miles (3.2 km.) or more the theoretical error is less than the practical error which is less than 0.5 inches in 100 feet. A much more difficult question was to find a suitable reference point from which to start the transect for there are no convenient surveyor's bench marks on these shores. In practice the actual level of the water at the low water of springs was used as the zero mark but it is realized that this is not a reliable datum and for this reason no conclusions are based on the transects which demand an accurate tidal datum.

On sandy shores the contour between high and low tide was first surveyed and then quantitative collections and records of environmental conditions were made at selected stations. The density of the epifauna was determined by hand-collecting and counting all organisms with a circle of 1 metre radius, the numbers being subsequently reduced to numbers per square metre. The density of burrowing forms was determined by digging out to spade depth all the sand within an area of 33×33 cm., putting it through a sieve and finally counting individual species and expressing the results in numbers per square metre. *Callianassa*, which is one of the most important organisms on the sandbanks, burrows much deeper than spade depth and lives in sand which is too 'sloppy' to determine the number of animals per burrow or number of exit holes per animal. There was, in fact, no satisfactory method of determining its absolute density so that only the number of holes per square metre is given.

The depth of the water table at low tide: If the water table is within an inch of the surface a hole made by a pencil and left for five minutes gives a good impression of the water-level. If the water-table was deep a narrow hole was dug with a trowel until wet sand was reached and then left until the water-level had risen as far as it would go at the time of low spring tide.

Sand temperatures: The temperature in the surface of the sand was taken at different levels. By 'surface' is meant the temperature recorded when the bulb of

the thermometer is just concealed. By 'temperature at 3 inches' is meant the temperature recorded when 3 inches (7.6 cm.) of thermometer stem is below the sand.

Salinity was determined by the usual Knudsen's methods.

Analysis of sediments: In general the methods used are those described by Morgans (1956). Where appropriate the median particle size ($Md\phi$) is given in millimetres as well as the degree of sorting in terms of $QD\phi$.

When surveying a rocky shore the contours and the level of convenient reference points above the zero mark were first determined and then the upper and lower limits of each of the common organisms was fixed. The uppermost specimens of most species occur in pools or trickles where the full effects of desiccation are minimized. It is emphasized that such specimens were not included in the survey. Finally the varying density between these limits was determined by eye as present, common, abundant, etc. No attempt was made to estimate density in terms of numbers per unit area as neither time nor tide permit this, and in most areas the irregularities of the rock surface make this method impossible.

DESCRIPTION OF THE AREA

Saldanha Bay is situated on the Atlantic coast of South Africa about 60 miles (96 km.) north of Cape Town and its centre is 33° S. 18° E. As shown by the accompanying map (fig. 1) it is open to the south-west. The anchorage at Saldanha (Hoedjes Bay) is protected but the coastline between there and Langebaan village is open to the surf and Lynch Point is particularly exposed. South-west of Langebaan village there is a channel leading to Langebaan lagoon. Both are completely protected from oceanic swell by a long finger of land parallel to the coast and by Meeuw and Schapen Islands which guard the entrance channel. The lagoon itself is about 9 miles (14.4 km.) long, 1-2 miles (1.6-3.2 km.) wide and seldom more than a fathom (1.8 m.) deep at low tide.

The climate of this part of the western Cape is warm and very dry. Annual temperatures range from a minimum of 5.1° C. at night in winter to a maximum of 34.0° C. at midday in summer and the annual rainfall normal for the past forty-five years is 9.76 inches (248 mm.). Most of the soil is sandy and as a result the countryside is covered with drought-resistant scrub, low bushes and a great variety of succulents. Although there are extensive marshes in the low-lying areas around Botlary, no rivers enter the lagoon and the farmers and villagers depend on natural springs, artesian wells or rain-water. Indeed, it was the absence of adequate water supplies in the vicinity of Saldanha Bay which decided the early colonists on settling around Table Bay and not around the much safer harbour of Saldanha.

The geology of the area is interesting. The rocks at Lynch Point, Schapen Island and the channel are granite but the low reefs around the lagoon are soft *Dorcasia* limy sandstone containing numerous semi-fossilized marine shells such as might be expected to live in a sheltered bay or estuary. Moreover large areas of the channel bed are sand covering a 3-foot thick layer of semi-fossilized oysters which are

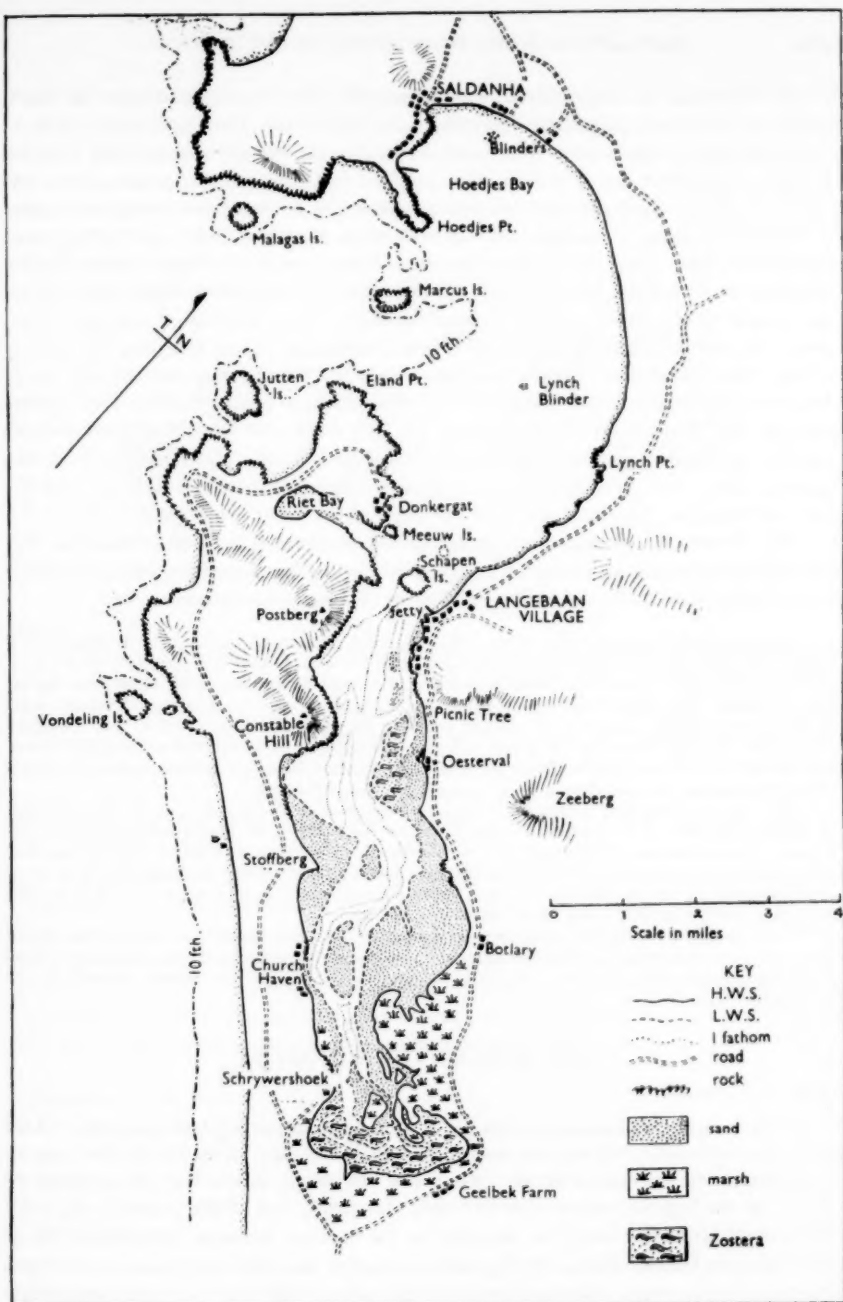


FIGURE 1

Chart of Saldanha Bay—Langebaan lagoon. Modified from Admiralty Chart 1232 (Saldanha Bay) with corrections to 1956.

dredged, ground up and exported as chicken grit. The oysters have been identified as *Ostrea atherstonei*, originally recorded as a fossil from the Quaternary beds at Alexandria in south-eastern Cape and more recently recorded alive from Knysna Estuary and False Bay by Korringa (1956). Apart from two samples from the Saldanha Bay-Langebaan area, no living oysters are known from the Atlantic coast of South Africa and the suggestion has been made by Haughton (1931) that in past geological times when the Cape Flats were below sea-level, warm water flowing northwards from False Bay drained into the Atlantic in the Langebaan area. When the level of the Cape Flats rose this supply of warm water was cut off and the oysters died. Another fascinating suggestion is that Langebaan lagoon was once the estuary of the Great Berg River which now flows into St. Helena Bay well to the north. Whatever the truth of these suggestions, it is certain that a carpet of sub-fossil oysters extends the whole length of the lagoon for they have also been dug from the salt marshes at Geelbek and are reported in Saldanha Bay near the Blinders. It is also certain that a very deep submarine canyon extends from the 100-fathom (180 m.) line off Saldanha Bay southwards to the edge of the continental shelf.

Dr. S. H. Haughton, who published his observations on the Saldanha Bay deposits in 1931, has kindly given me permission to reproduce here part of a recent letter to me concerning the geological history of Langebaan lagoon.

'Palaeontological evidence led me to conclude that the submerged shell banks in the lagoon, with *Ostrea atherstonei* and *Turritella capensis*, are older than the consolidated limestones above sea-level, and that all along the west coast there is evidence of differential warping of the older (and higher) beach deposits. The axes of the downwarps appear to be at or near the mouths of the major rivers (Groen, Zout, Olifants) and to strike at right angles to the coast; and it may well be that the downwarping at Saldanha was taken advantage of by a coastward-flowing river. Rogers visualised depression of the seaward ends of the Groen and Zout valleys, which became drowned, and the formation of lagoons at their mouths. The same must surely be true at Saldanha.

The history of the area is complex. The phosphatization of the granite and *Dorcasia* limestone at Hoedjes Bay and of the Langebaan ridge argue for the existence of these features as islands subsequent to the formation of the limestone. At Hoedjes Bay the limestone is cut by faults normal to the coastline; and the present inlet to the bay may have been determined by faults and be a down-faulted passage (a "trough" on a small scale); on the other hand it may be a normal mouth kept open through a sandbar behind which there was formed a lagoon.

The two suggestions made by you are not alternatives, as I read them; they may well be supplementary. I have no reason to doubt that the older deposits of the west coast do contain a warm-water fauna comparable with the modern fauna of the south-east and that the younger deposits do not contain that fauna.'

THE MARINE ENVIRONMENT

Tides and Currents

The normal tidal range at springs in Saldanha Bay is 5.3 feet (1.6 m.). There is a diurnal tidal cycle but no noticeable tidal currents. This is not the case in Langebaan lagoon and channel. When the tide turns in the Bay the imprisoned waters in the lagoon must escape and they ebb swiftly out of the channel, and tidal currents of up to five knots are reported in the narrows between Langebaan village and Schapen Island. Before the lagoon has emptied the tide starts to rise in the open bay and for this reason there is a reduced tidal range in the lagoon and a considerable

lag between the times of high and low tide in the bay and the lagoon. The tidal constant for Schrywershoek is quoted by the Admiralty tide table as 40 minutes after Table Bay but our own records, though taken over only a few tides and without any equipment, suggest that the low tide lag at springs at the head of the lagoon is much greater than this and that the tidal range is reduced to 56 inches (1.4 m.). The average of four observations are given below but it is known that the level of this large body of enclosed water is greatly affected by the prevailing winds which sweep the whole length of the lagoon.

TABLE 1. SPRING TIDE DATA FOR LANGEBAAN LAGOON
(Tidal range in inches and lag in minutes after Table Bay (standard port))

Position	Lag at H.W.S.	Lag at L.W.S.	Range
Langebaan village	0 min.	10 min.	67 in. (1.7 m.)
Oesterval	15 min.	30 min.	63 in. (1.6 m.)
Geelbek	47 min.	112 min.	56 in. (4.4 m.)

Wave Action

As will be shown, differences in the strength of wave action have a profound effect on the distribution of the fauna of both rocky shores and sandbanks. For this reason particular attention was paid to the average height of the waves on different shores.

It should be stressed at the outset that even the most exposed shores of Saldanha Bay at Lynch Point are never subject to the full force of oceanic waves. At Lambert's Bay to the north one may see the spray from a wave breaking on a rocky point driven 50 feet (15 m.) up into the air while the white surf boils below. None the less a careful assessment of wave heights at Lynch Point showed that the average waves were 2 feet (0.6 m.) from trough to crest while occasional waves up to 4 feet (1.2 m.) high occurred now and then. We were assured that at this time the bay was exceptionally calm.

As one moves further south towards Schapen Island and Langebaan village one comes into the shelter of Eland Point and the waves are reduced. On the northern (exposed) side of Schapen Island we have not seen waves higher than 2 feet (0.6 m.) and they are usually less. On Langebaan village beach the waves are seldom more than 6 inches (15 cm.) while in the channel and the lagoon oceanic swell is no longer appreciable. When the wind is quiet there is scarcely a ripple on the shore though the prevalent south-easter can make boating unpleasantly wet.

The Clarity of the Water

The water in the lagoon is very clear and the bottom is usually visible at a depth of 6 feet (1.8 m.) or more. In the deeper channel, Secchi disc readings of 7.5 feet (2.3 m.) have been made in winter and 11.7 feet (3.6 m.) in summer.

The Substratum

The chart shows that the bed of Saldanha Bay is mainly sandy though there are extensive rocky patches in the mouth and occasional outcrops approach the

TABLE 2. ANALYSES OF SUBSTRATA

Locality	Tidal level	M ϕ	Diam. (mm.)	QD ϕ	Description	Notes
Lynch Point	L.W.S.	-0.3	1.1	0.88	v. coarse sand	Stake 3: 28% CaCO ₃ ; 10% potassium felpar; very rounded sand grains and smooth shell fragments. No silt.
Trausket	Stake 3	0.9	0.55	0.58	coarse sand	
	H.W.S.	1.0	0.5	0.53	medium sand	
Langebaan village	L.W.S.	3.1	0.12	0.30	v. fine sand	Stake 2: 39% CaCO ₃ ; 0% potassium felpar; angular sand grains and shell fragments; echinoderm spines, foraminifera; sponge spicules. No silt.
Trausket	Stake 2	3.06	0.12	0.35	v. fine sand	
	Stake 4	3.2	0.13	0.26	fine sand	
Oesterval transect	L.W.S.	2.3	0.21	0.82	fine sand	Mid tide: 5% CaCO ₃ ; 1% potassium felpar; large rounded and smaller angular sand grains and shell fragments. 0.6% silt.
1957	M.S.L.	2.5	0.17	0.79	fine sand	
	H.W.S.	2.95	0.14	0.50	fine sand	
Centre bank opposite	L.W.S.	3.0	0.14	0.55	fine sand	Zostera level: Larger rounded and smaller angular sand grains and shell fragments. Few sponge spicules and foraminifera.
Oesterval	Zostera level	3.0	0.14	0.45	fine sand	2.0% silt.
Geelbek	L.W.S.	2.35	0.2	0.45	fine sand	M.S.L.: 6% CaCO ₃ ; 0% potassium felpar; well-rounded sand grains; few shell fragments; no foraminifera, sponge spicules or echinoderm spines. 8.2% silt.
	M.S.L.	2.30	0.21	0.48	fine sand	
	H.W.N.	2.37	0.2	0.58	fine sand	
<i>Bottom samples:</i>						
1. Off Langebaan jetty		1.15	0.45	0.83	medium sand	S.W. Constable Hill: 36% CaCO ₃ ; 5% potassium felpar; rounded sand grains; much shell; few echinoderm spines and foraminifera. 0.1-0.2% silt.
2. Off Postberg		1.70	0.32	0.85	medium sand	
3. S.W. Constable Hill		2.15	0.25	0.58	medium sand	

surface as blinders. Our own dredging was limited to the shallower areas where the bottom is fine well-packed sand except in more protected coves such as Donkergat where the bottom is softer and loose algae accumulate. Around Schapen Island the bottom is very variable. Details of the analyses of all substrata are shown in Table 2 and only the main features are given below. In the swift tidal channels the bottom is of smoothly rounded shell fragments and medium sand but in the lee of the island finer sediments accumulate and even soft black mud with rotting algae. Further up the channel there is a good deal of limestone and the bottom sediments are a little finer but poorly sorted. There are stones and fossil oysters mixed with medium sand and broken shell. Finally the channel broadens out into the shallow lagoon covered with medium sand and loose algae (*Gracilaria*). At Schrywershoek, towards the head of the lagoon, silt is mixed with the fine sand which becomes grey and discoloured.

The shores show more dramatic changes. At Lynch Point the shores are steep with enormous granite boulders well polished and rounded by the abrasive action of sand-laden waves. There are also low-lying reefs but these are so overgrown with the tube-building polychaet *Gunnarea capensis* that details are uncertain.

The sandy beaches near by are also very steep. The grades vary from very coarse sand at L.W.S. to medium sand at H.W.S. It is obvious that enormous masses of sand are continually being moved by the waves which have polished every pebble and rounded every shell fragment.

On Schapen Island the granite rocks are very uneven so that there are ridges and pools, boulders, shady crevices and overhangs but hardly a smooth slope suitable for a transect. Langebaan village beach opposite Schapen Island consists of very fine clean sand and shell fragments. There is no silt and individual fragments are very angular. The beach is well compacted and slopes up to a crest at high tide where drift weed accumulates. Behind this there is an extensive back beach.

As one proceeds up the channel the rocky shores become steep or even precipitous but there is a fair amount of silt between the loose stones and the coves have little sandy beaches which suddenly fall away at low-tide mark where the tidal currents keep the channels scoured.

In the lagoon the picture changes entirely. The only rocky patches are very low reefs of sandy *Dorcasia* limestone which are partially covered by sand from year to year. The sandbanks themselves tend to slope down fairly steeply to mean sea-level and then flatten out into enormous waterlogged areas of fine sand so riddled with *Callianassa* holes that one sinks in up to the knees. Most of the sand is fairly clean but muddy areas occur here and there and these are overgrown with *Zostera* at lower levels or salt marsh vegetation higher up. In backwaters such as Riet Bay and towards the head of the lagoon from Botlary to Geelbek these high-tide salt marshes cover enormous areas. From mid-tide down there are extensive sand or mud flats often overgrown with *Zostera*. The fine sand has the same median particle diameter as the rest of the lagoon but the records show that the silt fraction may make up as much as 6% of the total.

TABLE 3. SURFACE TEMPERATURES (°C.) AND SALINITIES (‰): SALDANHA-LANGEBAAN

	Saldanha	Shapen Is.	Channel	Oesterval	Church Haven	Schryvershoek	Geelbek	Salt Marsh Creeks
	L.W. H.W.	L.W. H.W.	L.W. H.W.	L.W. H.W.	L.W. H.W.	L.W. H.W.	L.W. H.W.	L.W. H.W.
<i>Winter:</i> (June, July, August)	13.9°C. (18)	13.4° 14.6° (3) (2)	13.2° (? tide) (2)	13.8° 14.0° (4) (4)	13.5° (? tide) (1)	No record	9.9° 18.0° (1) (1)	No record
	34.67‰ (1)	34.82 34.77 (2) (2)	35.61 (? tide) (1)	34.7 34.8 (2) (2)	No record	No record	32.66 33.16 (1) (1)	No record
<i>Spring:</i> (September, October, November)	15.4°C. (3)			No records				
	34.87‰ (3)							
<i>Summer:</i> (December, January, February)	16.9°C. (5)	18.4° 16.7° (4) (2)	21.8° 16.0° (2) (1)	18.0° 14.7° (2) (2)	23.9° 23.9° (2) (1)	22.4° 24.0° (2) (2)	22.9° 24.0° (4) (2)	27.3° (1)
	34.91‰ (3)	35.42 — (3) (3)	35.84 34.98 (1) (1)	36.60 35.60 (4) (4)	38.55 37.14 (1) (1)	39.21 38.39 (1) (1)	39.63 — (2)	42.11 (1)
<i>Autumn:</i> (March, April, May)	14.7°C. (5)	15.5° — (6)	16.3° (? tide) (3)	18.7° 16.2° (5) (5)	17.8° (? tide) (1)	16.9° 18.3° (1) (1)	20.8° 22.3° (1) (1)	24.0° 27.3° (1) (1)
	34.62‰ (1)	35.06 34.82 (6) (2)	— 34.86 (1)	35.2 34.9 (2) (3)	34.6 (? tide) (1)	36.4 36.6 (1) (1)	35.96 36.77 (1) (1)	41.04 (1)

Salinities and Temperatures

Records were collected from April 1946 to January 1958 whenever time and facilities permitted. A preliminary analysis showed that high and low tide values differed considerably and many data taken on the ebb or flow were thus discarded. The rest have been summarized in Table 3 which shows average high and low tide salinities and temperatures at each station for each of the four seasons of the year. The number of records from which each average is derived is shown by the small figures.

An initial inspection of the whole table will show that the hydrographic conditions in Saldanha Bay are more uniform and stable than they are in Langebaan lagoon. This is not surprising for Saldanha Bay is deeper and open to the ocean while Langebaan lagoon is enclosed and very shallow. Diurnal heating and cooling, evaporation and dilution by rain show marked effects on the temperature and salinity records.

Reference to Table 3 shows that during the winter temperatures throughout the bay and lagoon are fairly uniform, and range from 13.9° – 14.6° C. Records from the head of the lagoon at Geelbek show a variation from 9.9° C. at low tide to 18.0° C. at high tide. These extremes are merely part of more extensive records given in Table 4 which shows the results of nocturnal cooling and daily warming.

On 23/7/53 observers were posted at the entrance of the channel (Langebaan jetty), in the middle of the lagoon (Oesterval) and at the head of the lagoon (Geelbek). They recorded surface temperatures at regular intervals from low tide in the morning to high tide in the afternoon on a bright sunny day.

TABLE 4. RECORDS OF SURFACE TEMPERATURE ON 23/7/53

Time and Tide	Temperature ($^{\circ}$ C.)		
	Langebaan Jetty	Oesterval	Geelbek
07:45 (L.W.S. Langebaan)	13.5	13.5	—
08:10 (L.W.S. Oesterval)	13.0	13.5	—
08:30	13.5	14.2	9.9
09:25 (L.W.S. Geelbek)	13.9	14.0	10.0
10:30	13.9	14.0	13.6
11:30	14.0	14.0	15.0
12:30	14.2	14.0	16.5
13:30	14.7	14.0	15.0
14:30	14.6	14.0	18.0

Table 4 shows that in the narrow channel entrance (Langebaan jetty) there are minor variations ranging from 13.0° – 14.7° C. due to turbulence and upwelling. Indeed the swirls and eddies are obvious to any observer. At Oesterval in the quiet lagoon conditions were very uniform (13.5° – 14.2° C.) while at the head of the lagoon the shallow water had been cooled during the night to 9.9° C. and then as the rising tide flowed over the sandbanks warmed by the sun, the temperature gradually rose to 18° C. Other data have shown that all intertidal sandbanks cool during the night

but it will be noted that this nocturnal cooling is not appreciable in the deep channels at Oesterval where relative constancy is maintained by the much larger volume of water. None the less the nightly cooling and daily warming over shallow sandbanks must result in density changes in the overlying water and possibly assists in the aeration of interstitial water in the sandbanks.

With the daily warming effect in mind, let us consider Table 3 once more. The records here show that the warming effect is more marked in summer and autumn than it is in winter. This is because the shallow waters in the lagoon are not replaced with each tide but merely move up and down the channel like a piston and get warmer all the while. The surface temperatures in Saldanha Bay (mainly extracted from the reports of the Division of Fisheries) show that the annual range here is from 13.9°C . in winter to 16.9°C . in summer. At Oesterval in the lagoon the annual range is from 13.8°C . in winter to 18.7°C . in autumn, while at Geelbek at the head of the lagoon the range is from 9.9°C . at low tide in the early morning in winter to 24.0°C . at high tide in summer and in creeks draining the neighbouring salt marshes the temperature may rise to 27.3°C . Another interesting point is that in the channel and lower part of the lagoon the temperatures are higher at low tide as the warm lagoon water moves outward and lower at high tide when the cool Saldanha Bay water flows into the lagoon. At the head of the lagoon the tidal effect is reversed and the highest temperatures occur when the flood tide moves up over the sun-warmed sandbanks.

The salinity changes due to evaporation or rain in the lagoon are equally interesting. Saldanha Bay figures vary within the limited range of 34.62‰ – 34.91‰ . In the lagoon, however, the salinities are usually higher as a result of evaporation, though at Geelbek low salinities (32.66‰ and 33.16‰) were obtained after a winter rain and very high salinities (42.11‰) were recorded in salt-marsh creeks in summer. In the lower part of the lagoon the summer and autumn values show tidal changes as the more saline lagoon water and the less saline Saldanha Bay water moves to and fro.

It is important to mention that no consistent vertical gradients were noted in either temperature or salinity. It has been mentioned that the currents in the channel are very strong and the bottom contours very uneven. This gives rise to considerable turbulence. At times warmer and less saline water is recorded at the surface, but more usually there are no changes from surface to bottom and on some occasions there is denser (colder or more saline) water at the top than the bottom, showing that in spite of vertical eddies, mixing is not complete.

Summary of Physical Changes

Before considering the distribution of the fauna from Saldanha Bay to the head of Langebaan lagoon we may note that there are several marked physical changes. These are:

- (a) A marked reduction in wave action from 4-foot breakers at Lynch Point to mere wind ripples within the lagoon. Tidal currents are strong only in the channel.

(b) The shores change from clean rock to silt-covered reefs and from coarse sandy beaches which are steep and continually changing to permanent sandflats of fine sand or mud.

(c) As is usual in estuaries and lagoons temperatures change from cold and fairly uniform at the mouth in Saldanha to warm and variable at the head near Geelbek. The change is most marked in summer and autumn.

(d) Apart from the extremely variable salinities of salt-marsh creeks at the head of the lagoon, the salinities in open water are all within the normal sea range. The salinity of open waters at the head of the lagoon is slightly higher than that of the open bay but Langebaan lagoon is definitely not an estuary.

THE VEGETATION

Although no attempt has been made to survey the vegetation in detail, some account of the algae and halophytic angiosperms is necessary as a background to faunistic studies. A general picture of the vegetation is given below and more detailed accounts of particular transects will be found under the relevant headings.

Saldanha Bay

Apart from minor details the rocky shores of the bay have a normal west coast vegetation similar to that described for Lambert's Bay by Stephenson and Day (1940). Patches of *Porphyra capensis* occur at upper levels, but below these the rock is mainly bare to about low water of neaps where a mixed carpet of various species may appear including *Laurencia* sp., *Aeodes orbitosa* and *Chaetomorpha* sp. 'Lithothamnion' is well developed but *Champia lumbricalis* which usually forms a well-marked band above the kelp is very sparse here. The giant kelps *Ecklonia maxima* and *Laminaria pallida* grow well but *Macrocystis* was not found.

Sandy shores of Saldanha Bay are devoid of growing vegetation—in fact the only thing to be seen is a drift line of cast-up kelp and *Gracilaria confervoides* which provide food and shelter for small crustacea and insects.

Schape Island and Langebaan Village Beach

With increased shelter from wave action the algal covering of rocky shores becomes more luxuriant. It is not that new species appear for there is no obvious change in species composition, but the rocks at mid-tide tend to be more completely covered by a downward extension of *Porphyra* (on the outer side of the island) and an increase in *Chaetangium erinaceum* and *Ulva*. Near low tide the cochlear zone is often replaced by *Gigartina radula*. Below low tide *Ecklonia maxima* is still dominant.

Neighbouring sandy shores are still bare below the drift line.

Channel Rocks and Sandbanks

With the elimination of wave action there are marked changes in the algal flora. *Ecklonia maxima* and *Laminaria pallida* disappear entirely and the only common plants left are *Porphyra capensis* at the top, *Chaetangium erinaceum* on sandy rocks, and then *Ulva* sp. and *Aeodes orbitosa* forming green and olive bands towards low tide.

Sandbanks lose their bare appearance. A few scattered plants of *Chenolea diffusa* appear at the high-tide mark, then there is a long stretch of bare sand at the

lowest levels of which *Ulva* grows on any sort of solid object such as the mussel beds in mid-channel or occasional stones on the banks. *Gracilaria confervoides* grows from low tide downwards and *Zostera capensis* first appears towards the top of the channel where it opens out into the lagoon. The detailed distribution of both of these plants has been described by Isaac (1956) and further notes are given below.

Lagoon Reefs and Sandflats

There are only few low limestone reefs in the lagoon and they are often covered with sand towards low tide. The lowest levels of the reefs at Oesterval are fringed by a creeping *Laurencia* and by what may prove to be the attached stage of *Gracilaria*. There are also a few luxuriant plants of *Ulva* at the same level but above this the plants are very scrappy. Isolated plants of *Codium duthiae* and *Chaetangium erinaceum* occur here and there, but the general impression is bare rock though a closer inspection reveals a fairly thick film of black lichen. There is no *Porphyra*.

The sandbanks above mid-tide vary tremendously. Many are entirely bare with only a line of cast-up *Zostera* to mark the high-tide mark. Elsewhere extensive salt marshes may develop as at Botlary and Geelbek. These places are flatter and more muddy and the substratum is obviously less porous, so that the water table is near the surface and pools of standing water with *Enteromorpha* may be found. The usual sequence from extreme high water of springs downwards is as follows: On dry sandy banks the lawn-grass *Sporobolus virginicus* just reaches extreme high water of springs. In wetter areas various species, particularly *Salicornia Meyeriana*, *Limonium scabrum* and *Chenolea diffusa* extend further down to below H.W.S. The level between high water of springs and neaps is dominated by *Arthrocnemum perenne* with *Triglochin bulbosum* in wetter areas. Mixed with the *Arthrocnemum* but extending to lower levels where it just meets *Zostera capensis* is the rank grass *Spartina capensis*. This lawn-like vegetation, of course, affords food and shelter for a variety of small animals which will be discussed later.

The sandflats below mid-tide may either be bare or be covered to a greater or lesser extent by two plants—*Zostera capensis* and *Gracilaria confervoides* whose ecology has been described by Isaac (1956). *Zostera* is very patchy. Extensive fields grow on the centre sandbank opposite Oesterval at about low water of neaps. It also flourishes at the head of the lagoon around Schrywershoek, but elsewhere it is scanty. Some patches may grow at high water of neaps particularly where there is seepage from higher levels. In general it seems to prefer a more muddy soil. *Gracilaria* grows best at the channel entrance to the lagoon but its full range is from Church Haven to Langebaan village. It dominates infratidal levels to a depth of about 10 feet and also extends above low water of springs and scattered plants were recorded on the Oesterval transects 10–15 inches above L.W.S. where it mixes with *Zostera*.

The broad changes in intertidal vegetation may be summarized by saying that the most exposed rocky slopes are relatively bare and that moderate shelter from wave action increases the algal cover. However, when wave action is eliminated as in a dock basin the algae are reduced to species such as *Enteromorpha*, *Ulva* and

small filamentous forms. On the other hand exposed sandy beaches are bare and with increasing shelter halophytic angiosperms become more and more luxuriant.

THE DISTRIBUTION OF THE FAUNA

Appendix A, which is fully described on p. 514, shows the distribution and relative abundance of all species that have been identified. It is not a complete list since several groups such as the Porifera, Actiniaria, Polyzoa have not been completely identified. None the less it is felt that the list is well worth publishing for it represents the results of twelve years of collecting plus earlier records of sponges and nemertines. Many new species were found during the course of the work and many new records for South Africa. Apart from this, the list is the basic data for the analysis of distribution patterns which is one of the main objects of the paper.

VERTICAL ZONATION ON ROCKY SHORES

References to several papers on the zonation of the rocky shores of South Africa are given by Stephenson (1947). Probably the most suitable areas for comparison with Saldanha Bay are the accounts of Lambert's Bay to the north (Stephenson and Day, 1940) and Oudekraal to the south (Bright 1938). Apart from details, the vertical succession found on the granite slopes in Saldanha Bay agrees very well with these earlier accounts. However, none of the areas so far described is anything like as well sheltered from wave action as the rocky shores of Schapen Island or the rocky banks of Langebaan channel. Of the many transects that were surveyed, two contrasting ones are reproduced here to show the direct and indirect effects of wave action on vertical zonation. The methods used are described on p. 477 and it is stressed that records from pools or seepage channels were omitted from the survey so that the transects show the vertical distribution of organisms subject to the full effects of desiccation. The two transects are shown in figures 2 and 3. The vertical range and changing density of each important species is indicated.

Lynch Point where the first transect was made is an exposed point in Saldanha Bay subject to 4-foot (1.2 m.) waves even in calm weather. The transect shows the smooth seaward slope of an enormous granite boulder whose crest rises 140 inches (3.6 m.) above L.W.S. It was colonized by marine organisms to the very top and neighbouring shoreward boulders showed that *Littorina knysnaensis* and *Porphyra capensis* rose even higher. The *Porphyra* was bleached and became scanty lower down the slope where barnacles and limpets became common. On the flattish part of the slope there was a carpet of *Laurencia* sp., short tufts of *Ulva* and more luxuriant growths of *Aeodes*. Corallines appeared among scattered individuals of the ascidian *Pyura* just above the almost vertical face which led down to low-tide mark. This vertical face was covered with massed *Pyura* to which were attached large limpets (*Patella argenvillei*). Both were overgrown with barnacles. Half-way down the slope the kelps *Ecklonia maxima* and *Laminaria pallida* became codominants with *Pyura*.

The second transect shown in figure 3 was made on the south or sheltered side of Schapen Island. The rock here is also granite but has not been subjected to the

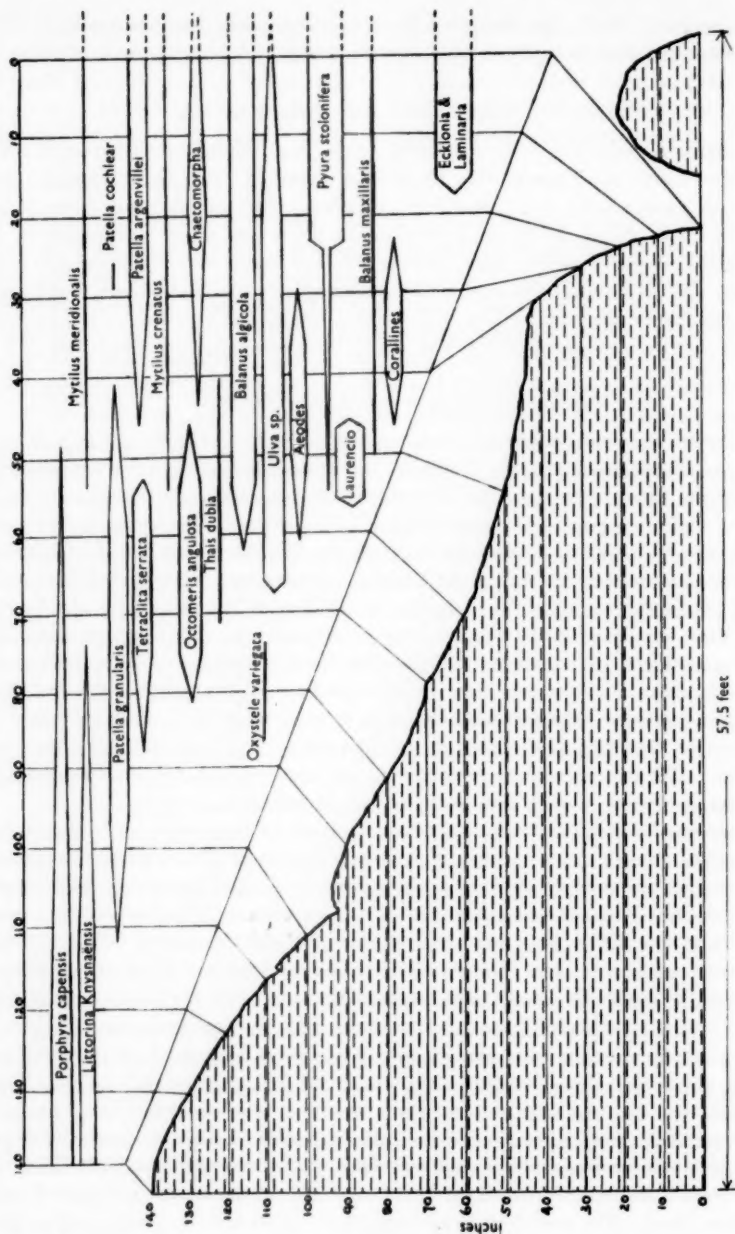


FIGURE 2

Transect over a granite slope at Lynch Point in Saldanha Bay. Vertical scale in inches above L.W.S.

abrasive action of sand-laden waves and the surface is very irregular with small pinnacles, vertical ledges, crevices, runnels and pools.

Just above low-tide mark large plants of *Ecklonia maxima* may be seen and a few *Laminaria pallida*. The uppermost holdfast of *Ecklonia* are exposed and soon dry as the water is very calm. Then as the tide seeps upwards it covers first a ridge of *Vermetus corallineus* and rather patchy 'lithothamnia', then clumps of mussels and large *Balanus maxillaris*, bright red anemones (*Pseudactinia flagellifera*), large olive plants of *Aeodes*, dark brown fronds of *Gigartina radula* and the green fronds of *Ulva*. Thereafter the water-level slowly covers the limpets, barnacles and periwinkles until it reaches the ledges along which hang skirts of *Porphyra*. Above this there are only a few more *Littorina knysnaensis*. The high-tide mark is easily fixed because the rock remains white with old bird droppings and the tiny pools are encusted with salt—evidence that at times a high tide coincides with an offshore wind.

The major differences between the two transects are of course due to differences in wave action, but before discussing this effect it is convenient to eliminate the confusing local effects of sand, shade and the nature of the rock surface.

As mentioned earlier the smooth slope of the Lynch Point transect has been abraded by sand-laden waves. Few crevices and no pockets remain in which gastropods such as *Oxystele variegata*, *Oxystele tigrina* or *Burnupena delalandii* can maintain their position when the tide is down. These species are common elsewhere on Lynch Point and well represented on the Schapen Island transect where the rock surface is more irregular.

On the other hand wandering limpets such as *Patella granularis* prefer extensive areas of smooth rock. They flourish on the Lynch Point transect and on certain flat rocks on Schapen Island but are not common on the broken surface of the transect.

Again the smooth slope of the Lynch Point transect provides no shade for such forms as *Chiton nigrovirens*, *Helcion pectunculus* and *Actinia equina* and they are absent. They are, however, well represented in shady overhangs of the Schapen Island transect. Shade reduces the severity of desiccation and it is usual to find the topmost individuals of many species in such situations. When comparing the upper limits of species on the two transects it is well to keep this point in mind.

Attention may now be directed to the direct effects of wave action. Several points are evident.

1. Marine organisms colonize the exposed Lynch Point up to its crest 140 inches (3.6 m.) above L.W.S. and some extend to even higher levels on shoreward rocks. The sheltered Schapen Island transect, on the other hand, is colonized to only 75 inches (1.9 m.) above L.W.S. In other words the upper limits of the marine fauna and flora are extended by swash and spray on exposed faces and limited to the high-tide mark on sheltered ones. This is in agreement with similar findings from many parts of the world.

2. Species such as *Littorina knysnaensis* and *Patella granularis* which live at upper levels have a greater extension of vertical range on exposed shores than do *Balanus maxillaris*, *Mytilus crenatus* and *Pyura stolonifera* which live at the bottom of the shore.

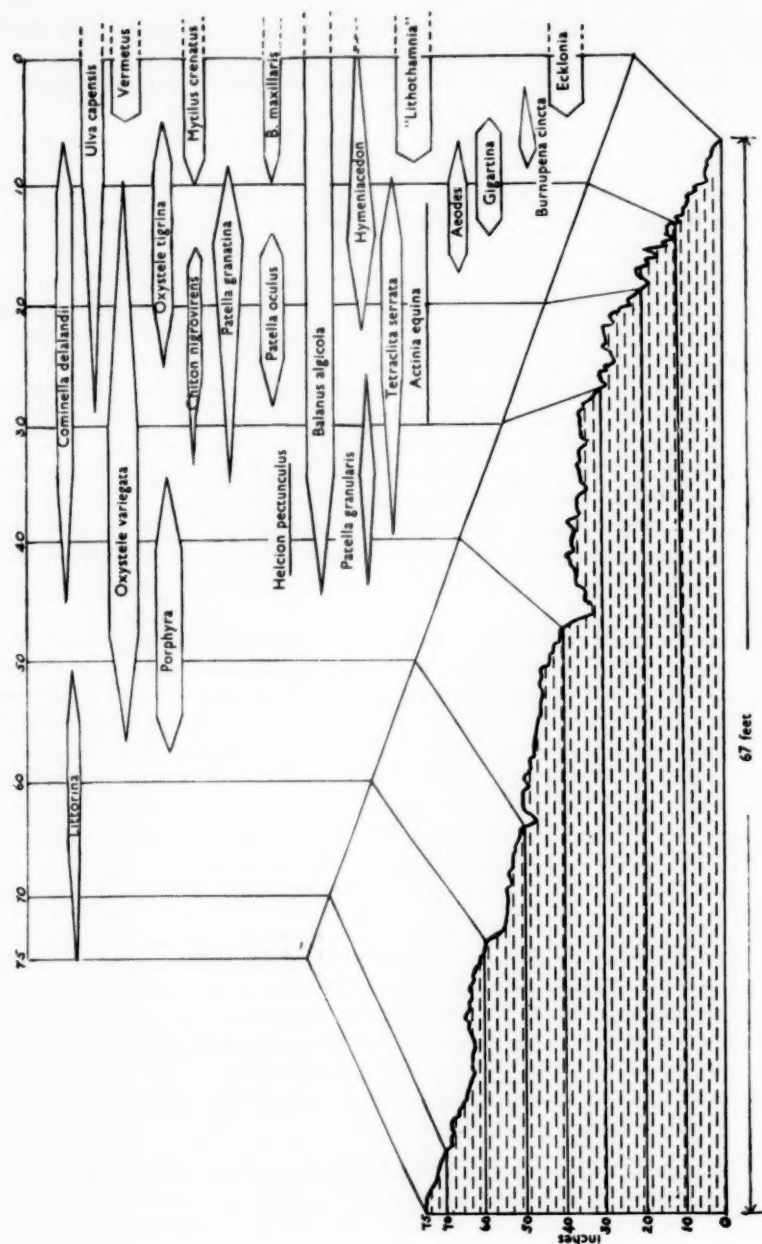


FIGURE 3

Transect over rocky shore on the south (sheltered) side of Schapen Island. Vertical scale in inches above L.W.S.

3. The absence of certain species (particularly gastropods) from smooth exposed rock faces has been noted earlier and a reasonable explanation offered. But the reverse is more difficult to explain. Several species such as *Patella argenvillei* and the barnacle *Octomeris angulosa* are absent from sheltered rocks and others such as *Pyura stolonifera* are greatly reduced in numbers. All of these animals (even *Patella argenvillei*) are effectively or actually sedentary so that competition for available areas of flat rock on which they can browse is not the answer. In the case of filter feeders such as the barnacle *Octomeris* or the ascidian *Pyura* it may be that the animal requires a considerable strength of water flow for its feeding processes. Recent work by Crisp on the feeding of barnacles affords some support for this suggestion and in the case of *Pyura* it was noted that the siphons are always orientated to the direction of the waves. The frequently quoted suggestion that exposed shore species are prevented from colonizing sheltered rocks by a reduction of oxygen concentration seems very doubtful because these surface waters are all supersaturated.

THE ECOLOGY OF SANDY SHORES

While a great deal has been written about rocky shores, relatively little has been said about sandy beaches, and certainly nothing has been published on South African conditions. A detailed analysis of the physical environment and its effect on the scanty fauna of surf beaches around the Cape Peninsula is now under way so no general discussion will be attempted here. However, the Langebaan-Saldanha area provides every gradation from an exposed surf beach to a quiet sandflat without any estuarine complication. It thus provides a good opportunity for investigating the effect of increasing shelter.

Apart from general collections to find the rarer species the ecology of the sandy shores was studied by means of surveyed transects in which the contours, grain size, temperatures, water tables, flora and fauna were analysed by the methods described earlier. Many transects were made and four contrasting ones are shown in figures 4, 5, 6 and 7 which are all drawn to the same scale to facilitate comparison. Incidentally this method of presentation stresses the marked differences in slope between exposed beaches (fig. 4) and sheltered ones (fig. 7). Analyses of substrata are given in Table 2 and these once again show obvious differences.

An exposed surf beach near Lynch Point (figure 4)

The waves here were mainly about 12 inches (30 cm.) high in calm weather but now and then a 3-foot (91 cm.) wave was seen. The intertidal part of the beach is very high (175 inches (4.4 m.) to H.W.S.) and slopes very steeply. It is composed of coarse to medium sand with rounded pebbles and smooth shell fragments, showing that the beach materials are in constant movement. Analysis shows no sign of silt and the drainage through the sand is so rapid that the water-table disappeared below the surface immediately above low tide. At 52.5 inches (133 cm.) above L.W.S. it was 10.5 inches (27 cm.) deep and at 89 inches it was 19 inches (4.8 cm.) deep.

The fauna was extremely scanty. A few mysids (*Gastrosaccus psammodytes*) were found at low tide but above this nothing until the drift line at the high-tide mark.

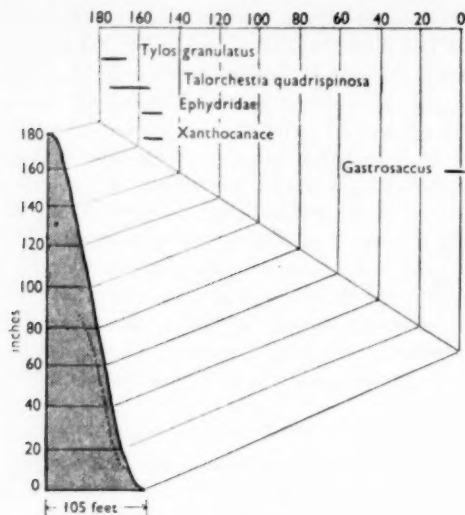


FIGURE 4

Transect over a sandy shore near Lynch Point in Saldanha Bay. Relative abundance and vertical and horizontal scales as in figures 5, 6 and 7. H.W.S. at 170 inches above L.W.S. Depth of water-table shown by dotted line.

Here there were a few talitrid amphipods (*Talorchestia quadrispinosa*), kelp flies (*Ephyridiae* and *Xanthocanace capensis*) and large nocturnal and semi-terrestrial isopods (*Tylos granulatus*). Nothing more was seen on the actual transect but the cast-up shells of *Donax serra* show that this bivalve is common in sandy coves between rocky promontories.

Langebaan Village beach (figure 5)

The waves here are about 3 to 6 inches (7.5 to 15 cm.) high but every now and then a long slow swell raises the water-level almost a foot. It should also be noted that the beach faces the channel which separates Schapen Island from the mainland and swift tidal currents flow along it. In conformity with the findings of Shepard and Inman (1951), it is thought probable that these currents are more important than the waves in shaping the contour of the shore, determining the particle size of the sands and carrying away the silt and detritus.

Between low- and high-tide mark the beach is 70 inches (1.8 m.) high and the contour is a fairly steep sigmoid curve but above high-water mark there is a flat back-beach. Details of grade analysis will be found in Table 2 but it may be noted here that the sand is very fine, well sorted and there is no trace of silt. The beach is firm and well compacted but drainage is still rapid for the water table leaves the

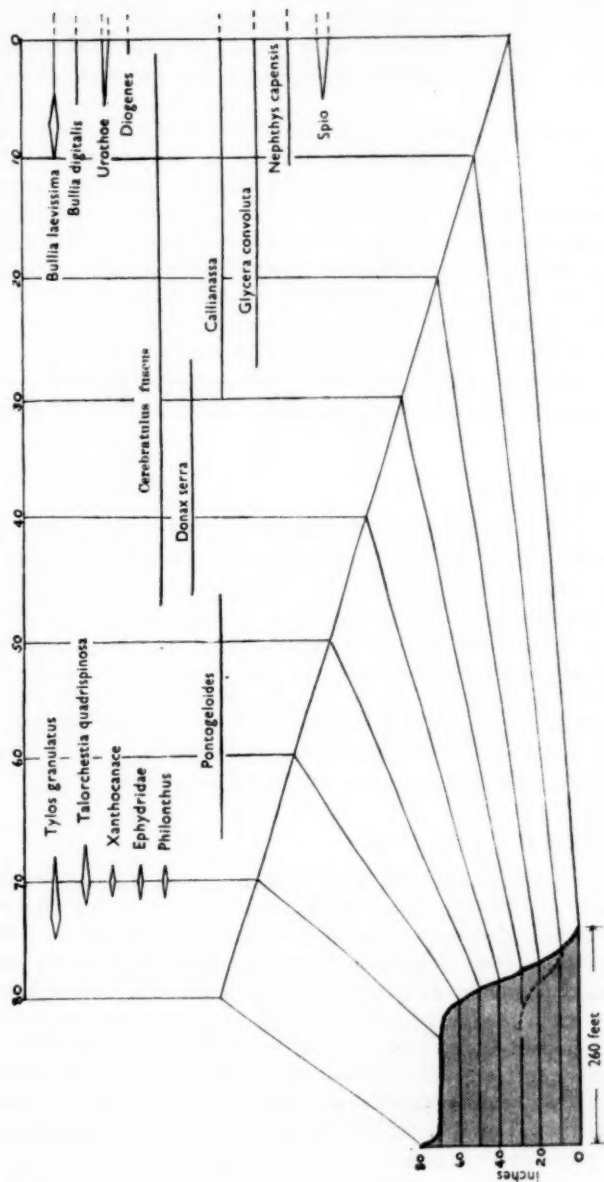


FIGURE 5

Transect over a sandy beach at Langebaan Village. Relative abundance and vertical and horizontal scales as in figures 4, 6 and 7. H.W.S. at 70 inches above L.W.S. Depth of water-table as shown by dotted line.

surface only 9 inches (23 cm.) above L.W.S. At and above H.W.S. the sand is relatively warm ($16.25^{\circ}\text{C}.$) but at mid-tide the temperature falls slightly to $15^{\circ}\text{C}.$ due to evaporation. As soon as the water table reaches the surface the temperature rises again ($15.3^{\circ}\text{C}.$). These differences, slight though they are, occur all along the shore.

Although 16 species are shown in figure 5 the fauna is really very scanty and is concentrated mainly at the top or the bottom of the shore. Several species including 5 surface forms occur at L.W.S. and extend up to the point where the water table sinks below the surface. Between there and H.W.S. there are 5 species 4 of which live in deep burrows which probably reach the water-table. At the high-tide mark there is another group of 5 species all capable of aerial respiration for long periods. These live under, and feed on, cast-up algae—mainly *Gracilaria* and *Ecklonia*.

General collections on sands of the transect revealed another interesting species at and below low-tide level. This was the pennatulid *Virgularia schultzei*. The only visible sign of the animal is a slender needle-like quill projecting above the sand but when dug out it becomes obvious that the animal can slide up and down on its own skeleton.

General Notes on Lagoon Sandflats

As explained earlier the extensive intertidal flats in the lagoon are completely protected from oceanic wave action though small wind-induced waves and ripples often occur. The substratum is fine sand with a varying admixture of silt and the surface may be practically devoid of vegetation or covered with *Gracilaria* and *Zostera* at lower levels and salt-marsh halophytes higher up. All of these factors affect the distribution and density of the fauna and a complete description of the lagoon fauna would occupy many pages. To save space most of this information has been summarized in Appendix A which shows the faunistic composition of lagoon sandbanks, *Zostera* beds and salt marshes. Two typical transects (figures 6 and 7) are described below and comments on *Zostera* beds follow.

Oesterval open sand transect 1954 (figure 6)

This transect was made across a sandflat which is so calm and undisturbed that the temporary survey stakes were still in place a year later. It runs from the high-tide drift line of cast-up *Zostera*, down a fairly steep sandy slope at the bottom of which a thin patch of *Zostera* is growing in seepage moisture and then out over 1,275 feet (390 m.) of flat sands. As shown, there are patches of *Zostera* and scattered plants of *Gracilaria* up to 18 inches (46 cm.) above L.W.S. The fine sand which was firm on the upper slopes becomes sloppy on the lower flats where the prawn *Callinassa kraussi* has made such extensive burrows below the surface that one sinks in up to the knees. The analysis shows that the particles are poorly sorted and that there is a small amount of silt. This is in marked contrast to what was found at Langebaan village. Shallow pools of water remain in depressions up to 18 inches (46 cm.) above L.W.S., and due to seepage from the steep upper slopes the water table is at the

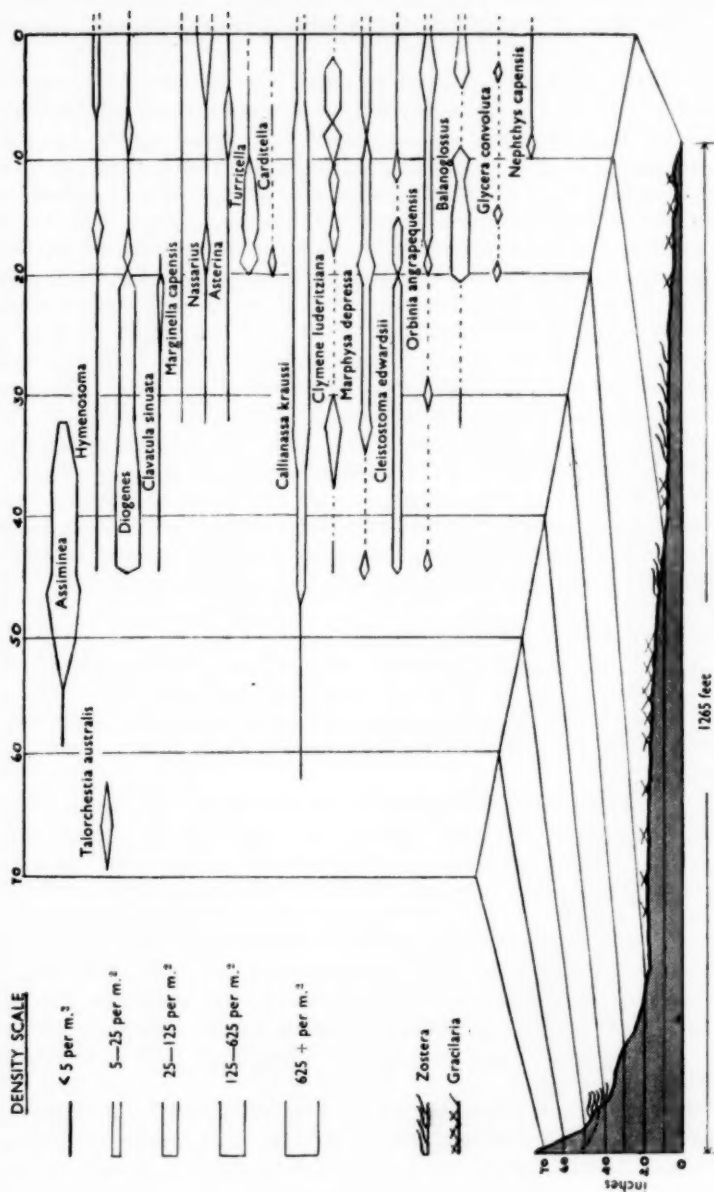


FIGURE 6

Transect across a sandy shore at Osterval in Langebaan lagoon. Relative abundance and vertical and horizontal scales as in figures 4, 5 and 7. H.W.S. at 70 inches above L.W.S. Depth of water-table as shown by dotted line.

surface 46 inches (120 cm.) above L.W.S. Sand temperatures vary from 16°–17·5°C., the lowest value (16·0° C.) being recorded from damp evaporating sand above the water-table.

The distribution of 20 of the 32 species which were identified and counted is shown in figure 6. There is no doubt that more work would have extended the upper limits of the less common species but the transect is 1,275 feet (390 m.) long and there was not time to work more than 17 sampling points. Surface forms are shown above and burrowing forms below. Of the former the most obvious elements are the minute Hydrobia-like gastropod *Assiminea globulus*, the hermit crab *Diogenes brevisrostris* and the whelk *Clavatula sinuata*. The crab *Hymenosoma orbiculare*, the whelk *Nassarius speciosa* and the filter feeding gastropod *Turritella knysnaënsis* are common but usually concealed just below the surface. Among burrowing forms it is obvious that the prawn *Callinassa kraussii* dominates the flats not only on account of its size and numbers but also because it burrows and continually brings fresh sand to the surface so that it conditions the environment for the rest of the fauna. The current of water which it draws below the surface must oxygenate the lower levels for there is no sign of blackening nor smell of H₂S. The smaller prawn *Betaeus jucundus* and the crabs *Thaumastoplax spiralis* and *Cleistostoma edwardsii* take temporary shelter in the mouths of *Callinassa* tubes even if they are not permanent commensals. Apart from *Callinassa* there are several species of small polychaets which are extremely abundant, particularly *Clymene luderitzi*, *Orbinia angrapequensis* and *Marphysa depressa*. Even *Balanoglossus* occurs in great numbers at its own preferred level.

Oestervl Salt-marsh Transect 1957 (figure 7)

In contrast to the 1954 transect made over open sand, the 1957 transect was made over a near-by salt marsh which was growing in more clayey soil in the lee of a low reef. Since the two transects are only a hundred yards apart conditions of wave action, salinity and surface temperature are the same; indeed, it is only the upper levels that differ.

The dry sandy soil above the intertidal zone is overgrown by xerophytic scrub with patches of lawn-grass *Sporobolus virginicus* here and there. This grass extends down to E.H.W.S. which is marked by a drift line of dead *Zostera* harbouring kelp-fly larvae (*Ephydriidae*) and beach hoppers (*Talorchestia australis*). Below this there is a break in the vegetation due to carts and tractors which have made a rough track at the top of the beach. Beyond this one reaches the salt marsh proper. This is dominated by the dense sprawling succulent *Arthrocnemum perenne* at upper levels and the rice grass *Spartina capensis* lower down. But these are not the only plants. Any slight elevation bears a patch of *Chenolea diffusa* or *Limonium scabrum* while the more soggy depressions and seepage channels show *Cotula coronopifolia* at H.W.S. or *Triglochin bulbosum* lower down.

This dense plant cover keeps the surface of the soil most even at midday and provides harbourage for several small surface animals. The commonest of these is the minute snail *Assiminea globulus* but *Littorina knysnaënsis* and *L. punctata* also occur at upper levels and with them are a few crabs (*Cyclograpsus punctatus*) and isopods

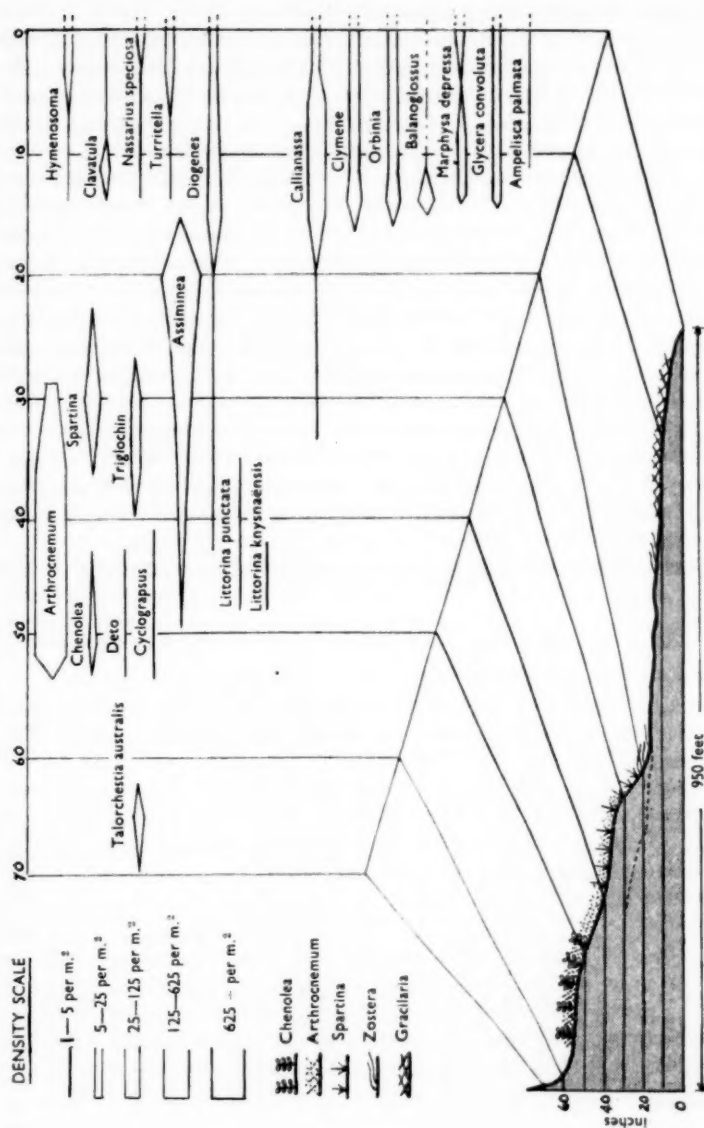


FIGURE 7

Transect over a salt marsh and sand flat at Osterval in Langebaan lagoon. Relative abundance and vertical and horizontal scales as in figures 4, 5 and 6. H.W.S. at 70 inches above L.W.S. Depth of water-table as shown by dotted line.

(*Deto echinata*). The moist shade also allows a few hermits (*Diogenes brevirostris*) to extend much higher than they do on open sandy beaches.

The substratum beyond the marshes is soft sand with small patches of *Zostera* here and there and numerous sprawling plants of *Gracilaria* at lower levels. The water-table is at the surface at 15 inches above L.W.S. and there are shallow pools in any slight depression. In general, conditions are similar to those found in the lower part of the 1954 transect and the fauna is essentially the same.

After the first few transects had been made over lagoon beaches attempts were made to relate the distribution of the fauna to tidal levels. It was soon found that this was hopeless as may be seen from even a cursory comparison of the 1954 and 1957 transects. In the 1954 transect (fig. 6) most species extend 33 to 45 inches (83 to 114 cm.) above L.W.S. while in the 1957 transect (fig. 7) most of them disappear 14 inches (36 cm.) above L.W.S. In the case of burrowing forms this may be due to the change in the nature of the substratum at the edge of the salt marsh but it is significant that in both cases the major change occurs just below the point where the water-table comes to the surface. Macnae (1956) and earlier workers have stressed the importance of the water-table in determining distribution on intertidal sandbanks, but as far as I am aware no objective evidence has been provided. In order to test the possibility that vertical distribution on a sandbank is more closely related to the depth of the water-table than it is to the height above

TABLE 5. UPPER LIMITS OF COMMON ANIMALS ON LAGOON BEACHES AND THE RELATION TO WATER TABLE

	Heights above L.W.S. (inches)					Heights above Water-table (inches)				
	Salt marsh		Bare		Max. Range	Salt marsh		Bare		Max. Range
	1955	1957	1954	1956		1955	1957	1954	1956	
EPIFAUNA										
<i>Diogenes brevirostris</i>	22	45	45	56	34	5	30	-2	0	32
<i>Hymenosoma orbiculare</i>	22	14	45	56	42	5	-1	-2	0	7
<i>Cleistostoma edwardsii</i>	30	43	45	52	22	12	28	-2	-4	32
<i>Clavatulina sinuata</i>	23	14	45	56	42	5	-1	-2	0	7
<i>Nassarius speciosus</i>	5	18	32	32	27	-13	3	-14	-20	23
<i>Assiminea globulus</i>	46	50	63	70	24	29	34	15	14	20
		Average			32		Average			20
INFUANA										
<i>Callianassa kraussi</i>	23	34	50	60	37	5	19	5	10	14
<i>Orbinia angrapequensis</i>	17	17	45	51	34	-1	2	-2	-4	6
<i>Marphysa depressa</i>	23	14	45	52	38	5	-1	-2	-4	6
<i>Clymene luderitzi</i>	14	17	45	52	38	-4	2	-2	-4	6
<i>Tellina triangularis</i>	0	—	8	17	17	-18	—	-39	-39	21
<i>Turritella knysnaensis</i>	23	14	45	56	32	5	-1	-2	0	7
<i>Balanoglossus capensis</i>	14	15	32	—	18	-4	0	-14	—	14
		Average			31		Average			11

L.W.S. table 5 was prepared. This shows both the maximum height above L.W.S. and the relation to water table of 13 species of animals on four different transects, two of which lay over salt marshes and two over bare sandbanks. In practically every case it will be evident that the upper limit is more closely related to the water-table than it is to the tidal level. Indeed, experience in the field and the changes in density suggest an even closer correlation between upper limits and height of water-table than is revealed by these figures. It may be that patchiness of distribution which is well known for *Balanoglossus* or insufficient sampling of rarer species like *Tellina triangularis* may explain the anomalies, but these two factors might affect height above L.W.S. as well as the relation to water-table. On the other hand it will be noticed that the poor correlation to water table shown by the hermit crab *Diogenes brevirostris*, the crab *Cleistostoma edwardsii* and the gastropod *Assiminea globulus* are due to upward extension in the shelter of salt-marsh vegetation. The essential point is that an animal's upper limit is determined not by its doubtful ability to measure heights above the surveyed datum but largely by its resistance to desiccation. It may escape the drying action of the sun and the wind by remaining below the level on the shore where the sand is saturated even at low tide or it may extend higher either in a burrow deep enough to reach the water-table (e.g. *Callianassa*) or, if it is a surface dweller, by sheltering in salt-marsh vegetation (e.g. *Diogenes*). The distribution of small animals like amphipods may further be restricted by the amount of water in the sand as Pennak (1942) found to be true for harpacticoid copepods in New England beaches, or by the permeability of the sand as Webb (1958) found for *Branchiostoma* at Lagos.

Zostera Beds

Zostera capensis occurs on various intertidal banks in the lagoon. There are luxuriant beds at the head of the lagoon at Geelbek and Schrywershoek and smaller patches nearer the channel. The one on the central bank opposite Oesterval has been studied most intensively. The *Zostera*, which is luxuriant with fronds about 12 inches (30 cm.) long, extends from the highest level of the bank (which is just exposed at L.W.N.) to low tide of springs where it is replaced by *Gracilaria confervoides* growing on clean sand. *Zostera* itself grows on black sandy soil smelling faintly of H_2S , though whether this type of substratum has been formed because of the presence of *Zostera* or whether the presence of suitable soil provides the right conditions for the growth of *Zostera* is unknown.

The *Zostera* beds have a fauna different from that of the surrounding sandbanks which are dominated and conditioned by *Callianassa*. The comparable burrowing prawn in the *Zostera* beds is *Upogebia africana*. As has been stated previously (Day, Millard & Harrison 1948) it is a filter feeder which makes permanent burrows in fairly firm mud and thus does not affect the tubes and burrows of other members of the infauna as does *Callianassa*. *Arenicola loveni* and *Marphysa sanguinea* are both common here, as well as several smaller polychaets, the bivalve *Tellina triangularis* and the small Synaptid holothurian *Taeniogyrus dayi*. Even occasional specimens of *Pyura stolonifera* whose tests develop roots like a turnip are lodged in this relatively

firm mud and in turn they provide support for a number of surface forms such as *Amblychilepas scutellum* and *Anthothoe stimpsoni*. *Mytilus meridionalis* is anchored to dead shells, and large growths of the sponge *Hymeniacidon perlevis* are scattered over the bank. More mobile forms shelter under the matted *Zostera* when the tide is down, but when the fronds start to float a sweep net provides a rich catch of Amphipods, isopods (particularly *Paridotea unguolata*), shrimps including *Palaemon pacificus* and *Hippolyte kraussiana*, and quite a number of pipe-fish (*Syngnathus acus*). For a full list of species and their relative abundance the reader is referred to the appendix. It will reveal many more differences between the fauna of *Zostera* beds and bare sandbanks. While these may be due to differences in substratum it is felt that equally important factors are the activities of *Callianassa* on the one hand and the shelter provided by the *Zostera* fronds on the other.

THE RESULTS OF DREDGING

The main work at Langebaan was done on the shore. None the less dredging parties were often sent out in a small boat driven by an outboard motor and the appendix shows that a good deal of material was collected and identified. The following brief notes give an appreciation of distribution of some of the common species but much more work must be done from a large boat provided with a grab before a systematic account of the fauna below tide marks can be presented.

The bed of Saldanha Bay is widely covered with fine well-packed sand into which the dredge would not 'bite'. The rather scanty collections which resulted suggested an epifauna of *Bullia laevissima*, *Nassarius speciosa*, *Synidotea hirtipes*, *Ophiothrix triglochis* and various scavenging amphipods of which *Lysianassa ceratina* was the most common. Loose algae such as *Ulva* and *Gracilaria* and mussels (*Mytilus crenatus*) tend to accumulate in sheltered coves such as Hoedjes Bay and Salamander Bay and the seaweeds and mussels provide shelter for shrimps (*Palaemon pacificus*), crabs (*Hymenosoma orbiculare*) and small squids (*Hemisepius typicus*). The ubiquitous *Cucumaria insolens* is also abundant here. Rocky patches were not well sampled for the little boat had insufficient power to pull the dredge, but the few samples indicate that *Mytilus crenatus*, *Parechinus angulosus*, *Ophiothrix triglochis* and *Balanus algicola* are present in quantity well below low-tide mark.

The channel bottom is very varied. There is almost sterile broken shell in swift channels, gravel patches with localized concentrations of *Ophioderma leonis* in more moderate currents, extensive sandbanks with *Macra adansoni*, *Thyone aurea* and numerous polychaets in the shallows and black mud with decaying algae and enormous numbers of *Cucumaria insolens* in the lee of Schapen Island. On one occasion we spent a morning on board the old barge which works a large grab for bringing up the subfossil shells of *Ostrea atherstonei* which when washed is sold to the United States for chicken grit. Each grab brings up the best part of a cubic metre of sand, stones and oyster shell which is put through a rotating screen. Many different animals were collected from the screen including densely packed colonies of *Polydora hoplura* in chunks of soft limestone, large numbers of *Thyone aurea* and many very large specimens of *Eunice aphroditois*, some nearly a metre long.

South of Constable Hill the channel widens out to form the large shallow lagoon whose bed is entirely covered with fine sand which becomes progressively more and more silty towards Schrywershoek and Geelbek. Most of the animals are small polychaets and amphipods but the records show that *Balanoglossus*, *Turritella knysnensis*, *Diogenes brevirostris*, *Nassarius speciosa*, *Hymenosoma orbiculare* and *Callianassa kraussii* are common well below the low-tide mark. Whenever *Gracilaria* is brought up there are always large numbers of *Paridotea unguolata* clinging to it. To judge by the concentrations of this isopod seen in night plankton samples, it must be one of the commonest herbivores in the lagoon.

THE COMPOSITION OF THE FAUNA

As shown on p. 487 three important environmental changes occur between Saldanha Bay and the head of Langebaan lagoon. These are first a reduction of wave action, second a change in substratum and third a rise in sea temperature. Equally marked biotic changes may reasonably be expected. The most striking changes in shore zonation have been described in the preceding pages and in those that follow an attempt will be made to analyse the changes in composition of the fauna throughout the system.

DESCRIPTION OF APPENDIX A

The basic data for this analysis are given in Appendix A which is an annotated faunistic list from 10 collecting stations on rocky and sandy shores and in 3 dredging areas. The list also shows the relative abundance at each station according to the following symbols: A = abundant, C = common, FC = fairly common, LC = locally common, and P = present. It will also be noted that each species has been given a 'faunistic category'—three code letters which summarize its depth range, geographical distribution and estuarine habits. Since these faunistic categories will be analysed in detail it is important to state how they have been derived and exactly what each code letter means.

The Department of Zoology of the University of Cape Town has been collecting records of the South African marine fauna for over twenty-five years and more recently these departmental records have been supplemented from the published literature with the help of systematists from all over the world who could advise on synonymy and doubtful records. The mass of data checked in this way has been used to give the 'faunistic category' of each species in the Saldanha-Langebaan area. The meaning of each code letter in the faunistic category is given below.

Depth Range (letters a-d and p)

The first of the three code letters in the faunistic category gives the depth range on the west coast of South Africa between the limits of Port Nolloth and Cape Point but excluding Langebaan which is the subject of this analysis. Depth records from other parts of South Africa or from other parts of the world were not considered as depth range may be affected by sea temperature.

- 'a' = shore only (i.e. not known from dredgings).
- 'b' = shore and dredged.
- 'c' = dredged only (i.e. not known from shore collections).
- 'd' = not known on west coast outside Langebaan.
- 'p' = pelagic.

Geographical Range (letters e-h)

The second of the three code letters gives the geographical range within the limits of South Africa but again excludes Langebaan records. For this purpose 'west coast' is defined as the sea or estuaries between Port Nolloth and Cape Point and 'south coast' means the seas or estuaries east of Cape Agulhas. Records from places between Cape Point and Cape Agulhas were disregarded as this stretch is an overlap between the west and the south coast.

'e' = west coast only (i.e. not known from the south coast).

'f' = west coast and south coast.

'g' = south coasts only (i.e. not known from the west coast).

'h' = Langebaan species not known from the west or south coasts as defined though it may have been recorded from the Cape Point-Cape Agulhas overlap area.

Estuarine Range (letters j-l)

The third of the code letters indicates whether or not the species has been recorded from South African estuaries.

'j' = estuarine only (apart from the present Langebaan records).

'k' = estuarine and marine—known both from South African estuaries and the open sea.

'l' = marine only (i.e. non-estuarine).

It will be evident that the code makes it possible to summarize a great deal of information for each species in the appendix and to discuss the changes in species composition between one part of the Langebaan-Saldanha area and another.

ANALYSIS OF SPECIES GROUPS

The first method of analysis is to divide the fauna of the whole area into three groups of species, one confined to the Saldanha part of the system and not extending past the northern shores of Schapen Island into Langebaan lagoon, one extending from Saldanha into Langebaan lagoon and one confined to Langebaan lagoon. It is then possible to compare the three groups of species to see how depth range, geographical range and estuarine range are affected by increasing shelter from wave action and rise in temperature.

Since the inclusion of dredging records would limit the conclusions which might be drawn from the data, the depth analysis is based on the distribution of shore species. There are 413 of these, of which 163 extend from Saldanha into Langebaan lagoon, 79 are restricted to Saldanha and 171 are restricted to the lagoon. Table 6 shows the percentage composition of each of these three groups in each of the four depth categories defined on p. 503.

TABLE 6. DEPTH ANALYSIS OF SHORE SPECIES

<i>Depth Category</i>	<i>Saldanha only</i>	<i>Saldanha and Lagoon</i>	<i>Lagoon only</i>
(a) Shore only.	53%	55%	35%
(b) Shore and dredged.	44%	44%	20%
(c) Dredged only.	1.5%	0%	15%
(d) Not known outside the Lagoon.	1.5%	1%	30%
Total shore species.	79	163	171

It will be seen that the depth range of species which spread from Saldanha Bay into the lagoon is very similar to the depth range of species which are restricted to the Saldanha part of the system. On the other hand the depth range of species which

are confined to the lagoon is very different. For example, the species which belong to depth category 'a' and are known only from the shore comprise 55% of the fauna which extends from Saldanha Bay into the lagoon, 53% of the fauna which is restricted to Saldanha but only 35% of the fauna which is restricted to the lagoon. Again in depth category 'c' which includes those species which *apart from these records* are known only from dredgings, 0% extend from Saldanha shores into the lagoon, 1.5% are restricted to Saldanha shores and 15% are restricted to the sheltered shores of the lagoon. This means that species which are known only from dredgings along the wave-washed shores of the west coast extend upward into the intertidal zone in the calm waters of the lagoon. It will also be noted that 30% of the shore fauna restricted to the lagoon is composed of species which are not known either from dredgings or wave-washed shores anywhere along the west coast. A more detailed analysis, which has not been reproduced here, shows that most of these species are south coast species while others are peculiar to Langebaan lagoon. The significance of all these findings will be discussed later after the rest of the evidence has been presented.

TABLE 7. GEOGRAPHICAL ANALYSIS

Category	Saldanha only	Saldanha and lagoon	Lagoon only
(e) West coast only	31%	19%	14%
(f) West and south coasts	53.5%	75%	45%
(g) South coast only	9%	5%	28%
(h) Others	6%	1%	14%
Total species	86	215	177

This geographical analysis is based on the total fauna of shore and dredged species though it may be noted in passing that an analysis of the shore species alone shows the same changes in an even more marked fashion.

It will be seen that the percentage of species belonging to category 'e' (i.e. those known only from the cold west coast) decreases between Saldanha Bay and the lagoon while the percentage of category 'g' (i.e. those known only from the warm south coast) increases. The composition of the fauna which extends over the whole Saldanha-Langebaan system shows a higher percentage of species belonging to category 'f', i.e. those common to both west and south coasts, and which may therefore be presumed to have a wider temperature range.

TABLE 8. ESTUARINE ANALYSIS

Category	Saldanha only	Saldanha and lagoon	Lagoon only
(j) Estuarine only	0%	2%	12%
(k) Estuarine and marine	16%	36%	21%
(l) Marine only	84%	62%	67%
Total species	86	215	177

This estuarine analysis is again based on the total fauna and again it may be noted that if dredged species are omitted the shore species show the same features in a more marked fashion.

It will be seen that the percentages of category 'j' (species which apart from these records are known only from Cape estuaries) increase in the sheltered lagoon while the percentage of category 'l' (non-estuarine species) is greatest in the exposed waters of Saldanha Bay. The highest percentage of category 'k' (estuarine and marine) is among species which extend from exposed to sheltered waters. It is concluded that estuarine species can live in a sheltered lagoon even though there is no reduction in salinity but cannot live on wave-washed coasts. Conversely many marine species drop out in sheltered lagoons.

ANALYSIS OF RECORDS

The second method of analysing faunistic composition is to consider how the distribution changes along a series of collecting stations covering different types of substrata and different degrees of shelter and to compare both shore and dredged records. In the previous set of analyses we were concerned with the composition of three groups of species but now we are concerned with the records at the different stations.

Table 9 has been prepared for this purpose and shows depth analysis, geographical analysis and estuarine analysis for 11 collecting stations covering rocky shores, muddy or sandy shores and dredgings in one table.* The total number of species identified from each station is shown in the bottom line while the penultimate line shows the number of common species. Reference to the literature—in particular to Stephenson (1944), Macfadyen (1957) and to Gunnar Thorson (1957)—shows that, in spite of some doubts, there is general agreement that analysis of faunistic changes should be based on the common or dominant elements of a fauna. It is such an analysis which has been made in Table 9 so that the percentages refer to the total of common species given in the penultimate line. Reference to Appendix A will show that each species which reaches to category 'common' in some part of the Saldanha-Langebaan system is marked with an asterisk. It is the records of these common species which are now being analysed.

An example will make the whole matter clear. In the last line of the first column it will be seen that 200 species have been identified from the rocky shores of Lynch Point. This total includes 77 common species. Depth analysis (lines a-d) reveals that 46 or 60% of them are known from shores only while 31 or 40% have been recorded both from shores and dredgings. Geographical analysis of the same 77 species (lines e-h) shows that 13 or 17% are restricted to the west coast, and 64 or 83% extend over both west and south coasts. Estuarine analysis of the 77 species shows that 1 (1%) belongs to category 'j'—estuarine only, 35 (46%) to category 'k' and 41 (53%) to category 'l'—non-estuarine.

Attention is first directed to the totals of common species which were recorded at each of the 11 collecting stations. On rocky shores it will be seen that the totals

* The 13 collecting stations listed in Appendix A have been reduced to 11 in Table 9 by combining the records from Lagoon sandbanks, *Zostera* beds and salt marshes under one comprehensive heading—'Lagoon sandy or muddy shores'.

TABLE 9. THE CHANGING COMPOSITION OF THE SALDANHA BAY-LANGEBAAN FAUNA BASED ON THE DISTRIBUTION OF COMMON SPECIES

	Rocky shores					Sandy or muddy shores			Dredgings		
	Lynch Point	N. side Schapen Is.	S. side Schapen Is.	Channel Rocks	Lagoon Rocks	Saldanha Bay	Langebaan Village	Lagoon	Saldanha Bay	Channel	Lagoon
DEPTH ANALYSIS*											
(a) Restricted to shores	46 60%	40 59%	38 58%	29 49%	21 53%	3 75%	2 18%	14 26%	1 3%	5 11%	5 18%
(b) Both on shores and in dredgings	31 40%	28 41%	25 38%	26 44%	16 40%	0 —	14 54%	20 36%	27 77%	28 64%	17 61%
(c) Restricted to dredgings	0 —	0 —	2 3%	2 3%	2 5%	0 —	2 8%	3 6%	5 14%	6 14%	4 14%
(d) None of these	0 —	0 —	1 2%	2 3%	1 3%	1 25%	8 31%	18 30%	2 6%	5 11%	2 7%
GEOGRAPHICAL ANALYSIS*											
(e) Restricted to west coast	13 17%	9 13%	10 15%	12 20%	5 13%	2 50%	6 23%	8 15%	8 23%	6 14%	6 21%
(f) Both on west and south coasts	64 83%	59 87%	54 82%	44 75%	33 83%	1 25%	14 54%	33 60%	24 69%	32 73%	20 71%
(g) Restricted to south coast	0 —	0 —	2 3%	3 5%	2 5%	1 25%	4 15%	10 18%	3 8%	4 9%	2 7%
(h) Known from Langebaan only	0 —	0 —	0 —	0 —	0 —	0 —	2 8%	4 7%	0 —	2 5%	0 —
ESTUARINE ANALYSIS*											
(j) Restricted to estuaries	1 1%	1 2%	3 5%	4 7%	5 13%	1 25%	6 23%	14 26%	2 6%	7 16%	5 18%
(k) Both in estuaries and the open sea	35 46%	35 51%	33 50%	35 59%	26 65%	1 25%	9 35%	20 36%	16 46%	20 46%	13 46%
(l) Restricted to the open sea	41 53%	32 47%	30 46%	20 34%	9 23%	2 50%	11 42%	21 38%	19 49%	17 39%	10 36%
Total common species	77	68	66	59	40	4	26	55	35	44	28
Total identified species	200	152	173	173	77	5	44	130	104	149	93

* Complete definitions of categories a-d in the depth analysis, categories e-h in the geographical analysis and categories j-l in the estuarine analysis will be found on pp. 503-4.

decrease from 77 at Lynch Point in Saldanha Bay to 40 on lagoon rocks. This decrease is paralleled by the numbers of all identified species from the same stations (200-77). It is thus obvious that far fewer species occur on sheltered rocky shores than on exposed rocky shores. Quite the reverse is true of sandy shores where the common species increase from 4-55 and the total identifications from 5-130. In dredgings the numbers 35-44-28 show no significant change. These conclusions regarding changes in number of species in different environment must be accepted with caution for more collecting in any one area would increase the figures quoted, though it seems unlikely that it would change the trends for the figures are based on ten years of collecting by large parties of students. None the less the validity of this type of criticism is accepted and all the analyses which follow are based not on actual totals but on percentages which are not subject to this type of criticism. Further, all the conclusions stated below have been tested for significance by the method of X^2 .

Depth Analysis (categories a-d of Table 9)

The object of this analysis is to determine whether there is any change in bathymetrical origin of the fauna of rocky shores, sandy shores or dredgings as one moves from wave-exposed stations in Saldanha Bay to sheltered stations in Langebaan lagoon.

On Rocky Shores: There is no significant change in bathymetrical origin of the fauna though there is a slight decrease in the percentage of category 'a' species on lagoon rocks.

On Sandy Shores: The penultimate line of Table 9 shows that only 4 common species were found on sandy beaches of Saldanha Bay, 26 from Langebaan village beach and 55 from sandbanks in the lagoon. The small numbers from Saldanha Bay do not permit direct statistical comparison between this exposed beach and the sheltered sands of the lagoon but indirect evidence can be obtained. It has been shown above that there is no significant difference in the rocky shore faunas in regard to depth range. Statistical comparison of rock and sand faunas in the lagoon now show that there is a significant difference between the faunas of these two substrata and that the percentage of category 'a' species is lower on lagoon sands than on lagoon rocks; in brief the sand faunas do show a change in bathymetrical origin with increasing shelter.

The above conclusion may be confirmed and extended by considering the identity of the species on the exposed sands of Saldanha Bay and on the sheltered sands of the lagoon. On Saldanha Bay beaches the 4 common species are *Tylos granulatus* (a semi-terrestrial isopod), *Talorchestia quadrispinosa* (a semi-terrestrial amphipod), *Xanthocanace capensis* (a kelp fly) and *Donax serra* a shore bivalve. All of these reach Langebaan village beach but none of them extend into the sheltered lagoon. It is thus obvious that none of the 55 species on the lagoon sandbanks comes from exposed sandy shores and that the faunas of exposed sandy beaches and sheltered lagoon sandbanks are entirely different in origin. None the less Table 9

shows that 14 of the 55 species are restricted to exposed shores outside the lagoon. If they are not from exposed *sandy* shores they must have come from exposed *rocky* shores, and reference to catalogues of exposed rocky shores confirms this. The species concerned are usually found in rock pools with sandy bottoms or under stones or in sandy crevices. It would seem that conditions in such habitats are more akin to conditions on the sandy shores of a lagoon than they are to conditions on a surf beach.

Further consideration of the depth range of sandy shore faunas show that apart from a few category 'c' species which elsewhere are known only from dredgings, there are 18 (30%) from lagoon sandbanks which are not known either from the shore or dredgings on the west coast. Over half of these are south coast species which will be discussed later and the rest are new to South Africa and so far known only from Langebaan lagoon.

In Dredgings: Statistical analysis does not reveal any change in depth range between the faunas of the three areas. The dredgings are all from shallow water and it is not surprising that most of the species belong to category 'f' and are known not only from dredgings but the shore as well. When more dredgings have been made in the deeper parts of Saldanha Bay a more detailed analysis may reveal interesting changes along the length of the Saldanha-Langebaan system.

Geographical Analysis (categories c-h of Table 9)

The object of this analysis is to determine whether differences in temperature in the various parts of the Langebaan-Saldanha system affect the geographical composition of the fauna.

On Rocky Shores: There are no significant changes in the geographical range of the species from different parts of the system. Most of the species are common to both west and south coasts, there is a slight reduction of species confined to the cold west coast as one enters the warm lagoon and there are a few species from the warm south coast but the numbers are too small for statistical analysis.

On Sandy Shores: There are too few records from the sandy shores of Saldanha Bay to permit of statistical analysis but the records from sandbanks in the lagoon do not differ significantly from rocky shores in the same area.

The Dredged Fauna: There are no significant changes between the different dredging areas.

These findings will be discussed later when all the evidence has been presented.

Estuarine Analysis (categories j-l of Table 9)

One of the primary objects of this study was to determine how similar is the fauna of a sheltered arm of the sea such as Langebaan to that of a Cape estuary. In South Africa the faunas of estuaries are very different from those of adjacent seas. Is this difference due to changes in salinity or is it due to other changes such as wave action?

On Rocky Shores: The percentages show that as one enters the sheltered lagoon two statistically significant changes occur. First the percentage of species common to estuaries and the sea increases and secondly the percentage of species restricted to the open sea decreases. There is also an increase from 1% to 13% of species restricted to estuaries but the records are too few for statistical analysis.

Since there is no reduction of salinity in Langebaan lagoon it is concluded that the changes are due either directly or indirectly to absence of wave action.

On Sandy Shores: Once again there are too few records from the sandy shores of Saldanha Bay to permit direct statistical comparison with the records from lagoon sandbanks. But lagoon sandbanks are not significantly different from lagoon rocks whose fauna contains a large proportion of estuarine species ($13\% + 65\% = 78\%$).

The Dredged Fauna: There are no statistically significant changes between the three dredged areas and when this fact is considered in relation to the marked changes in shore faunas it may be argued that the factor which affects estuarine composition must be a surface factor. The most obvious one is the degree of wave action.

DISCUSSION

The evidence regarding the composition of the fauna has been stated as briefly as possible. Two methods of analysis have been used and certain conclusions have been reached in each case. It now remains to review these and to present a balanced picture.

From the Langebaan-Saldanha system 478 species have been identified. Of these 413 have been found on the shore and after ten years of collecting it has been found that exposed rocks are richer in species than sheltered rocks but exposed sands are poorer than sheltered sands. The relative richness of the dredging grounds is unknown.

The bathymetrical range of the shore fauna has been investigated and it has been found that the shore fauna of the lagoon differs from that of the open bay. The former has fewer species which are restricted to shores on exposed west coasts and quite a number of species which elsewhere are known only from dredgings. These differences between exposed and sheltered shores are mainly due to the changing composition of the sand faunas for sheltered rock faunas are merely impoverished versions of exposed rock faunas. On the other hand none of the species which occur on exposed surf beaches extend on to the sandflats and mudbanks of quiet lagoons. These sheltered sandflats are colonized partly by species which occur in pools and sandy crevices of exposed rocky shores, partly by species which have migrated upwards from below low-tide marks and partly by species which are peculiar to sheltered lagoons and estuaries.

The analysis of geographical range does not give such clear-cut answers. As one enters the warm and sheltered lagoon there seems to be a tendency for species restricted to the cold west coasts to decrease and a tendency for more south coast species to appear. But the analysis of common shore species did not show that the differences were significant so the conclusion must remain open.

The estuarine analyses both showed quite clearly that there is a strong similarity between the fauna of Langebaan lagoon and that of a Cape estuary. The salinity of Langebaan lies in the normal sea water range, temperature differences between Langebaan and Saldanha have little if any effect on faunistic changes so it is concluded that the stronger estuarine element in the Langebaan fauna is due to shelter from wave action and its indirect effects of the nature of the substratum. In brief it is suggested that estuaries are largely colonized by 'calm water' species.

It is probable that the calm water fauna which inhabits lagoons and extends up to the middle reaches of estuaries is more distinct in South Africa than elsewhere because of the sharp environmental differences between these calm waters and open surf-battered coasts. In countries where the coastline is broken by inlets, coves, bays and intervening capes and minor promontories, one type of environment shades into another and local differences in the fauna are not so striking. Again the statements made above must not be taken to mean that there is no true estuarine fauna, no group of species which is restricted to waters of low salinity. As stated by Day and Morgans (1957), the work that has been done in South Africa shows that there is such a group but it is a very small one and experience suggests that it only becomes important in the upper reaches of estuaries. It should also be noted that the conclusion that estuaries are largely populated by 'calm water' rather than 'estuarine' species is in conflict with the suggestions made by Hedgpeth (1957, p. 695) and must be borne in mind when interpreting palaeoecological conditions from fossil assemblages.

CONCLUSIONS REGARDING THE EFFECT OF SHELTER

As mentioned in the introduction the main object of this research was to determine the effect of shelter on a marine fauna. Some of these effects may be direct but many are indirect, acting through changes in several environmental factors. Thus it is convenient to deal with these first before referring to the changes in composition and distribution of the biota.

Physical Effects

Increasing shelter reduces the vertical height of the intertidal zone both on rocky and sandy shores until it corresponds with tidal range. The spray belt above is reduced more than the swash belt below.

Where rocks and sand are mixed, the sand-laden waves have an abrasive action which in extreme cases will eliminate all forms of life just above the level of the sand and at higher levels may produce smoothed surfaces. Sheltered rocks are not affected in the same way. With complete absence of waves and currents, fine silt is deposited over all hard surfaces.

Wave action on sandy beaches has several effects: (a) In areas of heavy surf the intertidal zone is narrow and steep and the contour is continually changing as large masses of sand are deposited on, or removed from the shore. Under sheltered conditions the intertidal zone is broad with extensive flat areas towards the low-tide mark. Such beaches are essentially stable. (b) Beaches subject to heavy surf are

composed of relatively coarse, well sorted and rounded sand-grains with little or no silt. As a result drainage is rapid and the water table low. On sheltered shores the sands are finer, less well sorted (unless there are strong longshore currents) and silt and detritus tend to accumulate. As a result they are not so well drained as surf beaches. (c) Due to the flatter slopes and reduced drainage, sheltered beaches tend to have a high water table, and shallow pools may remain high up in the intertidal zone due to seepage from the slopes above.

Moderate shelter increases the algal cover on rocks but the elimination of wave action causes a drastic reduction of most species. Sands exposed to heavy wave action are devoid of macroscopic vegetation but sheltered flats are often well covered with halophytic angiosperms.

Sheltered rocky shores are populated by fewer animal species than exposed rocky shores but with a few exceptions there is no essential change in the nature of the fauna—the one is an impoverished version of the other. The decrease in number of species is probably due to the reduction in number of biotopes, for an exposed rocky shore has not only 'clean' exposed promontories colonized by browsing limpets and filter feeders which depend on strong currents, but also gullies, and stones in pools under which a wide diversity of animals find shelter. On sheltered rocky shores there are few species of algae and the rocks tend to be covered with silt which eliminates most of the browsing gasteropods. Crevices under stones are filled with silt and the water movements are too slow for efficient aeration.

On sandy shores increasing shelter causes an enrichment of the fauna and marked changes in composition. The scanty fauna of exposed surf beaches is composed of a few highly adapted species. The fauna of sheltered sandflats is derived partly from the fauna of sandy pools and crevices on exposed rocky shores and partly from species which have migrated upwards from infratidal levels, but there is also a distinctive 'sheltered water fauna', not found on exposed coasts either above or below the low-tide mark. The enrichment of the fauna is probably due to the permanence of the substratum, the accumulation of detritus along with the silt and the high water table.

On both sandy and rocky shores of sheltered lagoons a high proportion of the species present is similar to those found in the middle and lower reaches of estuaries. The number of species restricted to environments where there is a reduction of salinity is very small.

Effects on Vertical Zonation

On rocky shores increasing shelter reduces the vertical range of intertidal plants and animals. This reduction is most marked for those species which colonize the upper levels since the spray zone is almost eliminated. On sheltered rocks the upper (but not necessarily the lower) limits appear to be more sharply marked on dry sunlit rock. For a detailed discussion of critical levels and the nature of the infratidal fringe the reader is referred to Morgans (1959).

On sandy shores there appear to be two communities of animals many of which make migrations up and down the shore with the tides. One community is at the

top of the shore and is capable of aerial respiration for long periods. Most of the species live under the shelter of the drift line and all depend on it for food. The other community is found low down on the shore and is dependent on aquatic respiration. Its upper limit appears to be more closely related to the height of the water-table than to tidal level although the two often run parallel on a shore with a uniform slope.

On exposed surf beaches the two communities are widely separated for the water-table only reaches the surface near the low-tide mark. Surface forms are thus found at the bottom of the shore at the time of low tide while burrowing forms dig very deeply to reach the water-table.

With increasing shelter it has been shown that the water-table may reach the surface higher up the shore and for this reason the upper limit of the aquatic community may be raised. If the shore is stepped with surface seepage at the bottom of each slope the distribution may be discontinuous, and if salt-marsh vegetation or mangroves are present to produce dense shade and reduce evaporation the aquatic community may extend high up the shore and even mix with the aerial community. It will be obvious that where these factors vary from place to place there will be no relation between tidal level and shore zonation.

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APPENDIX A

This is an annotated list of plants and animals which have been identified from the Saldanha-Langebaan system. The records are grouped under 5 collecting areas on rocky shores, 5 from sandy or muddy shores and 3 dredging areas. Relative abundance in each collecting area is shown by the following symbols:

A = abundant	LC = locally common
LA = locally abundant	FC = fairly common
C = common	P = present (but not common)

The last column shows the 'faunistic category' to which each species belongs. Broadly the first of the three code letters gives the depth range, the second gives the geographical range and the third gives its estuarine distribution. In determining the faunistic category all Langebaan records were excluded since they are the subject of analysis in this paper.

An exact definition of the various faunistic categories is given on pp. 503-4 but for easy reference the broad meaning of the symbols is given below:

Depth Range	Geographical Range	Salinity Range
a = shore only	e = west coast only	j = estuarine only
b = shore and dredged	f = west and south coasts	k = estuarine and marine
c = dredged only	g = south coast only	l = marine only
d = range not known	h = range not known	
p = pelagic		

For example, the faunistic category 'cel' indicates that apart from the present Langebaan records the species is known only from dredgings in the open sea along the west coast of South Africa.

An asterisk in the last column indicates that the species concerned is a common species somewhere in the Langebaan-Saldanha system and is one of the species included in the analysis shown in Table 9.

[illegible]

[illegible]

	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
PORIFERA														
<i>Haliclona anonyma</i> Stephens						P		P	P					bfl
<i>Haliclona hospitalis</i> (Stephens)												P		chl
<i>Hymeniacidon perlevis</i> (Mont.)	A	A	C	C	C				LC			P		•bfl
<i>Leucosolenia coriacea</i> (Mont.)				P										afl
<i>Leucosolenia</i> sp. LB. 392 C.													P	
<i>Myxilla arenaria</i> Dendy					P									bfl
<i>Oceanapia polysiphonia</i> Dendy				P	P									ahl
<i>Polymastia mammillaris</i> Müller	P	P	P	P										ahl
<i>Tethya aurantium</i> (Pallas)				P										agl
COELENTERATA: Hydrozoa														
<i>Aglaophenia pluma</i> (Linn.) v. <i>parvula</i> Bale.	P	P	P								P			bfl
<i>Cnidonema valleritini</i> (Browne)									P				P	acl
<i>Hydractinia altispina</i> Millard	P													acl
<i>Hydractinia carnea</i> (M. Sars)											P	P	P	cfk
<i>Kirkpatrikia pinnata</i> (Linn.)	P	P	P	P	P	P					P	P	P	bfl

	Langbeaan	Jetty		btk
<i>Obelia dichotoma</i> (Linn.)	P			bfl
<i>Obelia geniculata</i> (Linn.)	P			bfl
<i>Paragutya intermedia</i> Warren	P			a/k
<i>Plumularia lagenifera</i> Allman	P			bek
<i>Plumularia setacea</i> (Ell. & Sol.)	P			bfl
<i>Salaria articulata</i> (Pallas)	P			bfl
<i>Sertularella africana</i> Stechow.	P			a/l
<i>Symplectosiphus macrogonus</i> (Treb.)	P			bek
<i>Tubularia solitaria</i> Warren	P			a/fl
<i>Tubularia ussuriensis</i> Ewer	On hull of dredger working in channel			bfl
COELENTERATA: Octocorallia				
<i>Parerythropodium wilsoni</i> (Thomson)	P			dhl
<i>Virgularia schultzei</i> Kükht.			C	ecl
COELENTERATA: Hexacorallia				
<i>Actinia equina</i> Linn.	P	C	LC	a/k
<i>Anathoea stimpsoni</i> (Verr.)	C	C	LA	bfl
<i>Bunodactis reynaudi</i> (M. Edw.)	C	A	C	a/k
<i>Bunodosoma capensis</i> (Lesson)	C	FC	C	a/fl
<i>Corynactis annulata</i> Verrill	LC	FC	LG	bfl
<i>Pseudactinia flagellifera</i> (Hertwig)	FC	C	C	a/k

<i>Bugula calathus</i> Norman.		P	P										P				bf1
<i>Bugula neritina</i> (Linn.)			P										P	P			af1
<i>Cellepora avicularis</i> Hincks.		P															ahl
<i>Celleporella hyalina</i> (Linn.)		P															bfl
<i>Chaperia acanthina</i> Lamx.	P	P															afl
<i>Dakaria subovoides</i> (d'Orb.)		P	FC											P			afk
<i>Electra pilosa</i> (Linn.) v. <i>verticillata</i> (Lamx.)		P	P													FC		bfk
<i>Menipea triseriata</i> Busk.		P															afl
<i>Retepora</i> sp. LB. 17														P			
<i>Rhamphonotus inermis</i> (Kluge)		P															ahl
<i>Schizoporella</i> sp. LB. 336 D.		P															
<i>Smittina ? landsborovi</i> LB. 336 E.		P															ahl
BRACHIOPODA																		
<i>Kraussina</i> sp. LB. 524 P.	P																
ANNELIDA; Polychaeta																		
<i>Antinoe lactea</i> Day			P										P	FC	P		dhl
<i>Arabella viricolor</i> v. <i>caerulea</i> (Schn.)	P																bfk
<i>Arenicola assimilis</i> v. <i>affinis</i> Ashw.																LC	*ael
<i>Arenicola loeni</i> Kbg.													P	LC	FC		*dgj
<i>Audouinia australis</i> (Stimps.)	LC	C														P	*bff
<i>Audouinia tentaculata</i> (Mont.)	P		P											P	LC		*bft

	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
ANNELIDA: Polychaeta (continued)														
<i>Aulolytus tuberculatus</i> (Schmarda)			P					P	LC	P				acl
<i>Ceratonereis erythraeensis</i> Fauvel												P		*dfj
<i>Chaetopterus varicopedatus</i> (Renier)									P					afk
<i>Cirratulus chrysoderma</i> Clap.	P	P	P	P	LC				P					*afj
<i>Clymene glandularis</i> Day														dgj
<i>Clymene ludritziana</i> Aug.	P			P	P			A		P		P	P	*acl
<i>Clymene lumbricoides</i> Quatref.					P									afj
<i>Clymene saldanha</i> Day								LC	P					*dhl
<i>Dayrbranchus bipartitus</i> (Schm.)	P													bfi
<i>Daychone natalensis</i> (Kbg.)	P	FC	FC	P										bel
<i>Daychone violacea</i> (Schm.)		P	P											bfk
<i>Diopatra 'monroi'</i> (SB. 125 T.)											P			
<i>Diopatra</i> (unidentate) (SB. 135 H.)											P			
<i>Dodecaceria pulchra</i> Day	LC	LC		P										*afj
<i>Dorvillea neglecta</i> (Fauvel)		P						P						dgl
<i>Ephesia gracilis</i> Rathke											P			bel

<i>Ezeone foliosa</i> Quatref.						P	P					bfk
<i>Eulalia (Eumida) sanguinea</i> (Oersted)	..														afl
<i>Eulalia cf. trilineata</i> St. Jos.	P														bfl
<i>Eulalia viridis v. capensis</i> Schm.		P	P	P									afl
<i>Eonice aphroditiois</i> (Pal.)	FC	FC	P	P						P	LC	*bfk
<i>Eunoe assimilis</i> McL.					P							cel
<i>Euphrasynce capensis</i> Kbg.		P	P									bfl
<i>Exogone verugera</i> (Clap.)	P											acl
<i>Fiabelligera affinis</i> Sars.		P	P	P								bfk
<i>Glycera convoluta</i> Kef.						P	FC	FC			FC	cfk
<i>Gunnarea capensis</i> (Schm.)		LA	FC	P	P								*afl
<i>Harmothoe aquiseta</i> (Kbg.)		P	P	P	P						P		bfk
<i>Harmothoe fraser-thomsoni</i> McL.					P	P					P	P	bfl
<i>Harmothoe saldanha</i> Day								P	P				dhl
<i>Harmothoe (Lagisca) usahli</i> (Kbg.)	..							P	P				P	P	bfl
<i>Heterocirrus capensis</i> Monro		P	P		P								bfl
<i>Lepidonotus clava v. semitecta</i> Stimps.	..			FC	FC	FC	P							P	bfk
<i>Lumbrineris coccinea</i> Remeri		FC		P	P								afl
<i>Lumbrineris heteropoda</i> Marenz.											P		cel
<i>Lumbrineris tetraura</i> (Schm.)		P					FC	FC	C			P	*bfk
<i>Lycastis quadraticeps</i> Gay.													dhk
<i>Lysidice natalensis</i> Kbg.		FC	P	P	P	P							afl

	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
<i>Marphysa capensis</i> (Schm.)	FC	P					LC	C				?		bel
<i>Marphysa depressa</i> (Schm.)			P	P	P				LC			P		*dgl
<i>Marphysa sanguinea</i> (Mont.)					P									*dgl
<i>Myrianida phyllocera</i> Aug.					P									afk
<i>Naineris laevigata</i> (Gr.)	FC	P	P	P	P			FC				P	P	b/k
<i>Nephtys capensis</i> Day							P					P		b/k
<i>Nephtys hombergi</i> A. & M.-E.								P	P			P	P	cfk
<i>Nephtys sphaerocirrata</i> Wes.-Lund. ..												P		dgl
<i>Nereis caudata</i> (D. Ch.)												P		dgl
<i>Nereis operia</i> Stümp.	P		P								P			b/k
<i>Nerine citrullus</i> (D. Ch.)							P							afk
<i>Nicola macrobranchia</i> (Schm.)	P	P	FC	FC	FC		LC		P		FC	FC	P	*b/k
<i>Nicomache lumbicalis</i> (Fabr.)		P	P	P	P			P				P		afk
<i>Notomastus latericus</i> Sars.								C	P				P	*d/k
<i>Odontaspilis polyera</i> (Schm.)	P	P		P										b/k
<i>Orbinia angustequensis</i> (Aug.)							P	A	LC					*dgl

ANNELIDA: Polychaeta (continued)

[illegible]

[illegible]

[illegible]

	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
CRUSTACEA: Amphipoda (<i>continued</i>)														
<i>Laetmatophilus tridens</i> Brnd.		P										dgl
<i>Lemboides afer</i> Stebb.											P	dgl
<i>Lemboides crenatipalma</i> Brnd.											P	cel
<i>Lembos hirsutipes</i> Stebb.									P			dgl
<i>Lembos jassopsii</i> Brnd.	P					LA					A	*acl
<i>Leucathoe richiardi</i> Lesson						P	P		P	P	P	chl
<i>Leucathoe spinicarpa</i> (Abildg.)										P	P	bfl
<i>Lyianassa ceratina</i> (Wlkr.)	..	P	P		P		P	C	FC		C	FC	FC	*bfl
<i>Lyianassa variegata</i> (Stimps.)	..	P										P		acl
<i>Maera hiondellei</i> Chevr.	..	P			P									bel
<i>Maera inaequipes</i> (Costa)	..	P												bfl
<i>Maera vagans</i> Brnd.	..	P												bel
<i>Megalutropus agilis</i> Hoek	..												P	dgl
<i>Melita organosus</i> Brnd.	..	P	P								P			bfl
<i>Melita zylantica</i> Stebb.	..								P					dfj
<i>Nototropis guttatus</i> (Costa)	..										LC			*cek

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CRUSTACEA: Tanaidacea

[illegible]

	P	FC	FC	bfl
<i>Cymodoce valida</i> (Stebb.)				bfl
<i>Cymodocella pustulata</i> Brnd.	P			afl
<i>Cymodocella sublevis</i> Brnd.	P	FC		afl
<i>Deto echinata</i> Guerin		P		afl
<i>Dynamenella australis</i> Rich... .. .	LC			*ael
<i>Dynamenella huttoni</i> (Thomson)	C	P		*afl
<i>Dynamenella ocalis</i> Brnd.	P	P		afl
<i>Eurydice longicornis</i> (Studer)			P	bfl
<i>Exophaeroma antitrossii</i> Brnd.		P		afl
<i>Exophaeroma lylooctes</i> Brnd.				afl
<i>Exophaeroma kroussii</i> Tattersall	P	P	FC	afl
<i>Exophaeroma pallidum</i> Brnd.	P			bel
<i>Exophaeroma planum</i> Brnd.	P			bfl
<i>Exophaeroma porrectum</i> Brnd.	P			afl
<i>Glyptidotea lichtensteinii</i> (Kr.)		P		afl
<i>Gnathia africana</i> Brnd.			P	afl
<i>Gnatholena mandibularis</i> Brnd.	FC			afl
<i>Haliopharma coronicauda</i> Brnd.				cfl
<i>Iais pubescens</i> (Dana)	P			bel
<i>Idotea indica</i> M. Edw.				cel
<i>Idotea ziczac</i> Brnd.				cel
<i>Tarapsis curvicornis</i> (Nicolet)	P			afl

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	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category	
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon		
CRUSTACEA: Anomura															
<i>Callinassa rotundicaudata</i> Stebb.	..	P		P				P	A	C	P	P	FC	FC	dgl
<i>Diogenes brevivestris</i> Stimps.	..		P	C	C										*cfl
<i>Paguristes engyops</i> Brnd.	P		FC												acl
<i>Paguristes gomianus</i> M. Edw.	P		P	P								P	P	P	bfl
<i>Porcellana streptochelus</i> Stimps.	..			P					P			P	P	P	afk
<i>Upogebia africana</i> (Ortm.)	..								LC	P					*dfj
<i>Upogebia capensis</i> (Kraus)	..		P	P	P							P			bfl
CRUSTACEA: Brachyura															
<i>Cleistiostoma algerense</i> Brnd...	..													P	dgl
<i>Cleistiostoma edwardsii</i> McLeay	..								FC	C	FC				*dgl
<i>Cryptodromiopsis spongiosa</i> (Stimps.)	..	P	P	FC	P							P	P		bel
<i>Cyclograpsus punctatus</i> M. Edw.	..	C	C	C	C						FC				*afk
<i>Dehaaninus dentatus</i> (M. Edw.)	..											P	P		bfl
<i>Dromidia hirsutissima</i> (Lam.)	..		P	P	P							P			bfl
<i>Hymenosoma orbiculare</i> Desm.	..			P	P				P	C	C	FC	FC	FC	*bfl

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	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
<i>GASTROPODA: Prosobranchiata (cont.)</i>														
<i>Patella argenvillei</i> Kr.	A	P	P											*af
<i>Patella barbara</i> Linn.	G	FC	P	P										*af
<i>Patella cochlear</i> Born.	LA	FC												*af
<i>Patella compressa</i> Linn.	P	P	P											acl
<i>Patella granatina</i> Linn.	G	A	C	FC										*acl
<i>Patella granulata</i> Linn.	A	A	C	P										*afk
<i>Patella miniata</i> Born.	P	P	P											bfk
<i>Patella oculus</i> Born.	LC	C	C	FC										*afk
' <i>Purpura</i> ' <i>wahlbergi</i> Kr.			P	P										bfl
<i>Pyrene kraussii</i> (Sow.)	FC		P	P	P				P			P	P	af
<i>Siphonaria aspera</i> Kr.	FC	A	A	A	A									*afk
<i>Siphonaria capensis</i> Q. & G.	P	P												afk
<i>Siphonaria compressa</i> n. sp. Allanson									LC					*dhl
<i>Tectonatica genuana</i> (Rve.)	P			P				FC			P			bfk
<i>Thais cingulata</i> Linn.											P			bfl
<i>Thais dubia</i> (Kr.)	C	FC	P	P	P					P				*afk

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ECHINODERMATA: Holothuroidea

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	ROCKY SHORES					SANDY OR MUDDY SHORES					DREDGES			Faunistic Category
	Saldanha Bay	Exposed side of Schapen Is.	Sheltered side of Schapen Is.	Channel	Lagoon	Saldanha Bay	Langebaan Village	Lagoon sandbanks	Lagoon Zostera beds	Lagoon Salt-marshes	Saldanha Bay	Channel	Lagoon	
CHORDATA: Tunicata (continued)														
<i>Styela pupa</i> Heller			P	P	P						P	P		agl
<i>Trididemnum cerebriforme</i> Hartm. .. .			P	P	P									agl
CHORDATA: Pisces														
<i>Atherina breviceps</i> Cuv.											P	P		pfk
<i>Blennionimimus ootoides</i> (Cuv.)		P	P											agl
<i>Blennius cornutus</i> (Linn.)				P										agl
<i>Blennophis anguillaris</i> (C. & V.)				P										agl
<i>Callorhynchus capensis</i> Dumeril		P	P									C	P	•bfk
<i>Clinus superciliosus</i> (Linn.)														pfk
<i>Chaetodon marleyi</i> Regan					P									•bfk
<i>Chorichthys dentex</i> Bloch			P	P	P						P	P		bfi
<i>Dasypatis pastinacus</i> (Linn.)											P	P		chl
<i>Diplodus sargus</i> Linn.													P	pfk
<i>Gobius nudiceps</i> Cuv.				P	C			P	P			FC	P	•afk
<i>Gobius saldanha</i> Brnrd.								P				P		dhl

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ON SOME SOUTH AFRICAN PYCNOGONIDA OF THE
UNIVERSITY OF CAPE TOWN ECOLOGICAL SURVEY

By J. H. STOCK, D.Sc., Ph.D.

(Zoological Museum, Amsterdam)

(Communicated by J. H. DAY)

(With nine text-figures)

(Read June 18, 1958)

Six new species are described from South African waters: *Nymphonella lambertensis*, *Achelia barnardi*, *Nymphon modestum*, *Propallene crassimana*, *Anoplodactylus unilobus*, and *Pycnogonum angulirostrum*. Two other species, *Ammothella indica* Stock and *Achelia* spec. aff. *australiensis* (Miers), are recorded for the first time from South Africa. The genus *Hannonia* is synonymized with *Tanystylum*. Of the genus *Queubus* the hitherto unknown female is described; her anatomical details point to relationships with the Callipallenidae. Remarkable anatomical facts are mentioned in *Propallene crassimana* (numerous cement gland cones), and in *Achelia barnardi* and *Tanystylum brevipes* (both with a retractable proboscis).

Although the South African Pycnogonid fauna is known to a large extent through the works of Flynn (1928), Barnard (1954) and Stock (1956), a small collection of Pycnogonida collected during the University of Cape Town Ecological Survey contained several new and interesting forms. The collection was sent to me for identification at the initiative of Dr. J. H. Day, Professor of Zoology, Rondebosch.

Of great interest is the occurrence in South Africa of a new species of *Nymphonella*, a curious genus with transformed appendages known to infest bivalve molluscs. Another animal in the collection (possibly young *Hannonia*) parasitizes a polychaetous worm, a rather uncommon food for pycnogonids. Noteworthy also is the discovery of the female of the endemic South African genus *Queubus*. As this female has 10-segmented ovigers, we may assume relationship to *Pallenopsis* and *Hannonia*.

SYSTEMATIC ACCOUNT

Family AMMOTHEIDAE

Genus NYMPHONELLA Ohshima

Nymphonella lambertensis n. sp. Figure 1

1 ovigerous male, holotype. Lambert's Bay, 32° 04-3' S.; 18° 18-2' E. Dredge, 15 m., sand.
Jan. 16, 1957. (U.C.T. Ecol. Survey LAM.1.P.)

Description: Resembling *N. tapetis* Ohshima in general characters and anatomical details. The lateral processes bear dorso-distally 2 small tubercles, each sometimes

tipped with a spinule. A stronger projection on the posterior-distal margin of the lateral processes. Midway a small anterior, and a large posterior, projection occurs. Proboscis much shorter and more robust than that of *tapetis*, shorter than the cephalic segment.

Scape of chelifer with 2 small tubercles near its base, and 3 bigger tubercles at its distal end.

Palps probably with 11 basic segments; segments 10 and 11 split up into 13 short segments. Segment 7 of the non-transformed part is slender, 2.5 times as long as segment 6.

Oviger segments 7 to 10 with compound spines, according to the formula 12: 8: 9: 12. These spines are placed in a row. On segment 8 an additional row of 4 compound spines occurs. The compound spines are lanceolate; those of segments 7 to 9 are about 4 times as long as wide and bear 12 to 13 pairs of denticulations. The 10th oviger segment is produced into a pointed projection, which is most probably a rudiment of the terminal oviger claw.

The legs agree with those of *N. tapetis*, except for the 2nd coxae, which bear 3 rounded papillae on the dorsal surface.

Eggs in ribbon-like masses resembling those laid by certain species of *Doris*.

The characters not mentioned in this description agree completely with those of *N. tapetis*.

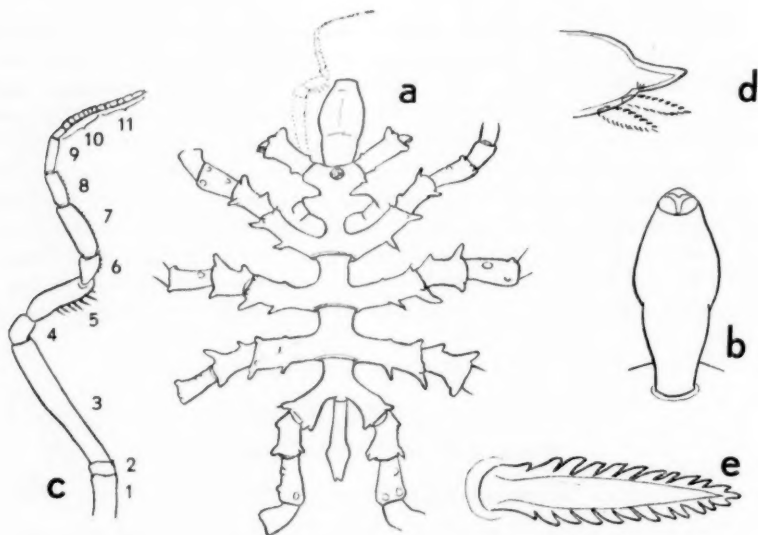


FIG. 1. *Nymphonella lambertensis* n. sp., ♂, holotype

a, trunk in dorsal view; b, proboscis in ventral view; c, palp; d, distal part of the terminal oviger segment; e, compound spine from oviger segment 8.

Remarks: This animal is very closely related to *Nymphonella tapetis* Ohshima, a curious pycnogonid found in Japan (Ohshima, different papers; Arita, 1936) and in the Mediterranean near Banyuls (le Calvez, 1950). Possibly the South African representatives of *Nymphonella* do not deserve a separate specific rank, but form a race (sub-species) of the typical Japanese form.

The South African *Nymphonella* differs from its Japanese allies in (1) the presence of strong projections in the middle of the lateral processes; (2) the presence of tubercles on the scape of the chelifers; (3) the relative length of the joints of the palp (in *tapetis* 'the segments 6, 7, and 8 are about of an equal length' according to Ohshima (1933, 56); in *lambertensis* segment 7 is 2.5 times as long as segment 6); (4) the oviger spines which are much more slender in *lambertensis* bear 12-13 pairs of denticulations (in *tapetis* about 8 pairs of denticulations); (5) the length of the proboscis (in *lambertensis* 1.36 mm. in ventral view, in dorsal view shorter than the cephalic segment; in *tapetis* more than 2 mm. long, longer than the cephalic segment); (6) in the presence of tubercles on the 2nd coxa.

The Mediterranean form is in some respects intermediate between the Japanese and the South African form.

Measurements of the male holotype

	mm.
Length (frontal margin cephalic segment to tip of abdomen)	3.9
Length (tip proboscis to tip of abdomen)	5.0
Width across the 2nd lateral processes	2.0
Length of abdomen	0.92
Length of proboscis (dorsal view)	1.08
Length of proboscis (ventral view)	1.36
Largest diameter of proboscis	0.51
Length of cephalic segment	1.01

Genus *AMMOTHELLA* Verrill

Ammothella indica Stock

Ammothella indica Stock, 1954, 113

1 female. Durban Bay. Scrapings from ships' hulls (working *only* in Durban Bay and tied up at Salisbury Island). Jan. 15, 1951. (U.C.T. Ecol. Survey DBN.132.V.)

This species was previously recorded only from the East Indies (Sunda Straits, Singapore).

Genus *NYMPHOPSIS* Haswell

Nymphopsis cuspidata (Hodgson)

Nymphopsis cuspidata, Barnard, 1954, 141

Lambert's Bay

- (a) 2 juveniles. 32° 05' S.; 18° 18.2' E. Dredge, 18 m., sand and algae. Jan. 21, 1957. (U.C.T. Ecol. Survey LAM.45.B-D.)

- (b) 1 female. 32° 05' S.; 18° 17·9' E. Dredge, 23 m., rock, shell, sand. Jan. 16, 1957. (U.C.T. Ecol. Survey LAM.7.X.)
- (c) 1 juvenile, in residue of various dredgings, depth between 11 and 27·5 m. Jan. 17-19, 1957. (LAM.16.R; 29.S; 21.X; 35P.Q.)

Langebaan Lagoon, 33° 05' S.; 17° 55' E.

2 ovigerous males, 2 females. Shore collection, outside of Schapen Island. Sept. 23, 1957. (U.C.T. Ecol. Survey LB.512.Q-R.)

Genus *ACHELIA* Hodge

Achelia quadridentata (Hodgson)

Achelia quadridentata, Barnard, 1954, 138

Lambert's Bay. 4 juveniles. 32° 05' S.; 18° 18·2' E. Dredge, 18 m., sand and algae. Jan. 21, 1957. (U.C.T. Ecol. Survey LAM.45.B-D.)

Saldanha Bay. 1 female, 2 juveniles. 33° 05' S.; 17° 55' E. Lynch Point. From kelp below L.W.S. Sept. 25, 1957. (U.C.T. Ecol. Survey SB.169.T.)

Achelia brevicauda (Loman)

Achelia brevicauda, Barnard, 1954, 140

Lambert's Bay. 2 specimens in residue of various dredgings between 11 and 27·5 m. Jan. 17-19, 1957. (LAM.16.R; 29.S; 21.X; 35.P-Q.)

Mossel Bay. 1 female, 1 juvenile. 10 min. rock dredge at 34° 08' S.; 22° 07' E. Depth 13·5 m.; sand and rocky patches.

Achelia spec., aff. *australiensis* (Miers) Stock

1 female, 2 juveniles. Lambert's Bay. 32° 05·2' S.; 18° 17·5' E. Bottom plankton, 30 m., sand. Jan. 19, 1957. (U.C.T. Ecol. Survey LAM.33.M-N.)

This is an unsegmented *Achelia*, resembling in most details *A. australiensis* (cf. Stock, 1954, 105). However, the small number of specimens does not permit of certain identification in such a difficult genus. Typical *australiensis* is only known from Port Jackson, Australia, and from Lyttelton, New Zealand.

Achelia barnardi n. sp. Figure 2

Mossel Bay

- (a) 1 female, holotype. 34° 10·42' S.; 22° 09' E. Dredge, 9 m., rock. Jan. 17, 1956. (U.C.T. Ecol. Survey MB.57.R.)
- (b) 1 male, 2 females, 1 juvenile. 34° 08' S.; 22° 07' E. Dredge, 13·5 m., sand and rocky patches. Jan. 19, 1956. (U.C.T. Ecol. Survey MB.69.M.)
- (c) 1 female. 34° 04' S.; 22° 14' E. Dredge, 17-20 m., coarse sand, shell, and rock. Jan. 18, 1956. (U.C.T. Ecol. Survey MB.61.L.)
- (d) 1 male, 1 juvenile. 34° 11·04' S.; 22° 10·9' E. Dredge, 16 m., sand to rock. Jan. 13, 1956. (U.C.T. Ecol. Survey MB.16.C.)

Description: Trunk without segmentation lines, although shallow depressions may sometimes be present between the trunk segments. Lateral processes armed with low tubercles. Eye tubercle conical, in juveniles more strongly pointed than in adults. Eyes well pigmented. Abdomen slightly curved upward, long, reaching to the distal end of coxa 1 of leg 4.

Proboscis elliptical in outline. Curiously enough, the proboscis appears to be retractile: its entire basal third may be retracted into the cephalic segment. In the preserved state, most specimens have the proboscis expanded, but some have it retracted. Of course, the general aspect of the animal is quite different when it is retracted or expanded.

Chelifers reduced, less than half as long as the proboscis. Scape terminating in some spine-bearing tubercles. Chelae reduced in adults, but chelate in juveniles.

Palps (fig. 2 *e-f*) 8-segmented, short and compact. Ovigera (fig. 2 *g-h*) 10-segmented in both sexes, those of male much stronger developed than those of female. The 6th oviger segment (male) with a strong reversed spine at its ventral margin. Segments 7 to 10 (male, female) bear compound spines.

Legs remarkable: In dorsal view (fig. 2 *j*) the pointed tubercles on the longer segments remind one more or less of the scales of a pineapple. Coxae 1 and 2 each with 2 dorsal tubercles. Genital spur (male) strong, present on the ventral surface of coxa 2 of legs 3 and 4. Genital pores (female) on the ventral surface of coxa 2 of all legs. Propodus strongly curved. Heel with 3 basal teeth, sole with short spinules. Near the distal end of the sole there is a strong tooth, forming a kind of subchela structure with the claw. No auxiliary claws.

Remarks: This is a very distinct species. The armature of the legs, the subchela propodus and the absence of auxiliary claws being sufficient to distinguish the species from all other members of this large genus.

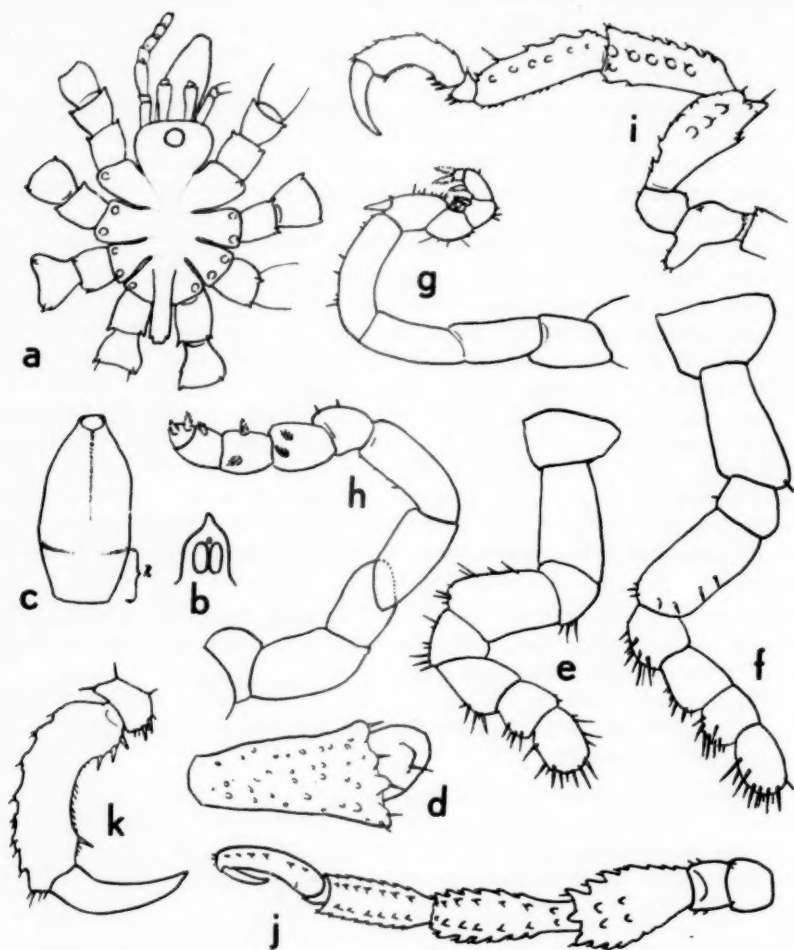
The species is named in honour of Dr. K. H. Barnard of the South African Museum, Cape Town, who has contributed so much to our knowledge of South African marine arthropods.

Measurements

							female	male
							mm.	mm.
Length (frontal margin cephalic segment to tip of abdomen)					1.2	1.3
Width across the 2nd lateral processes		0.79	0.88
Third leg, coxa 1	0.23	0.26
coxa 2	0.38	0.38
coxa 3	0.23	0.23
femur	0.79	0.75
tibia 1	0.72	0.72
tibia 2	0.72	0.75
tarsus	0.09	0.11
propodus	0.57	0.60

Achelia spec.

1 juvenile. Lambert's Bay. 32° 04.1' S.; 18° 18.35' E. Dredge, 16 m., rock. Jan. 16, 1957. (U.C.T. Ecol. Survey LAM.27.Z.)

FIG. 2. *Achelia barnardi* n. sp.

a, trunk in dorsal view (♀); b, eye tubercle, from the right; c, proboscis, in ventral view (the part marked R can completely be retracted into the cephalon); d, chelifer (♂); e, palp (♀); f, palp (♂); g, oviger (♂); h, oviger (♀); i, third leg (♂); j, dorsal aspect of the first leg (♀); k, distal segments of third leg (♂).

Genus *TANYSTYLUM* Miers*Tanystylum brevipes* (Hoek) nov. comb.*Discoarachne brevipes*, Barnard, 1954, 149

Lambert's Bay

- (a) 1 female, 1 juvenile. 32° 04.5' S.; 18° 18.3' E. Dredge, 17 m., sand and rock. Jan. 16, 1957. (U.C.T. Ecol. Survey LAM.2.Z.)
- (b) 1 female, 4 juveniles. 32° 05' S.; 18° 18.2' E. Dredge, 18 m., sand and algae. Jan. 21, 1957. (U.C.T. Ecol. Survey LAM.45.B-D.)
- (c) 1 male. 32° 09' S.; 18° 18' E. Dredge, 16 m., rock, sand and mussels. Jan. 23, 1957. (U.C.T. Ecol. Survey LAM.58.S.)
- (d) 1 female. 32° 05.5' S.; 18° 17.7' E. Dredge, 27.5 m., rock and shell. Jan. 19, 1957. (U.C.T. Ecol. Survey LAM.66.L.)
- (e) 7 specimens, in residue of various dredgings between 11 and 27.5 m. Jan. 17-19, 1957. (LAM.16.R; 29.S; 21.X; 35.P-Q.)

Saldanha Bay, 33° 05' S.; 17° 55' E.

- (a) 1 ovig. male, 1 male, 2 females, 1 juvenile. Lynch Point. From kelp below L.W.S. Sept. 22, 1957. (U.C.T. Ecol. Survey SB.152.A.)
- (b) 1 male, 1 juvenile. Same locality. Sept. 25, 1957. (U.C.T. Ecol. Survey SB.169.T.)
- (c) 1 juvenile. Lynch Point. Shore, from pools under granite boulders. Sept. 22, 1957. (U.C.T. Ecol. Survey SB.154.G-H.)

Langebaan Lagoon (part of Saldanha Bay)

- (a) 1 male. Under stones on south side of Schapen Island. Lower balanoid zone. May 5, 1951. (U.C.T. Ecol. Survey LB.298.M.)
- (b) 1 ovig. male, 2 females. Outside Schapen Island, shore collection. Sept. 23, 1957. (U.C.T. Ecol. Survey LB.512.Q-R.)

Table Bay

- 1 juvenile. 33° 52.5' S.; 18° 26' E. Dredge, 20.5 m. July 3, 1947. (U.C.T. Ecol. Survey TB.231.C.)

Remarks: The commonest South African Pycnogonid. It was hitherto always referred to *Discoarachne*, a monotypic genus considered endemic to South Africa. Having now had the opportunity of examining numerous specimens of both sexes, I am certain that the genus *Discoarachne* has no right of existence. The genus is synonymous with *Tanystylum*, described two years earlier (1879) by Miers.

The chelifers of *Tanystylum* are always in various degrees of reduction. In *Discoarachne*, this reduction proceeds so far that the chelifers become vestigial. In young specimens of *Discoarachne*, chelifer stumps are present and as strongly developed as in *Tanystylum*. In adults of *Discoarachne* these stumps usually persist, but sometimes they vanish completely. The number of palp segments in *Tanystylum* varies between 4 and 8, the 4- to 5-segmented palpi of *Discoarachne* fall within these limits. The female oviger of *Discoarachne* is identical with that of *Tanystylum*, whereas male ovigers of the same type as in *Discoarachne* occur also in certain *Tanystylum* species, e.g. in *Tanystylum hummelincki* Stock.

I see no reason to separate the two genera.

The proboscis of *Tanystylum brevipes* may be in various states of retraction. Thus, sometimes it appears nearly twice as long as the palps, sometimes as long as the palps. The proboscis is retractable in a cavity of the cephalic segment; a soft dermal zone ('cuff') at the base of the proboscis makes the retraction and expansion possible. The various aspects offered by specimens with retracted or expanded snouts complicates still further the taxonomic problems of this complex and variable species. Perhaps the epithet *brevipes* is merely a collective noun for those South African species of *Tanystylum* which have very short chelifer stumps and 4- to 5-segmented palps. In most specimens, the proboscis is more or less fusiform (as illustrated by Barnard, 1954). Those of Langebaan Lagoon have it more pointed (as in certain species of *Achelia*). The distal oviger joints (male) may be either very hairy (as illustrated by Loman, 1923), even without distinct 'terminal chela', or nearly smooth with a distinct 'terminal chela' (as illustrated by Barnard, 1954).

The species needs a careful revision, based on material collected throughout its range in South Africa.

Tanystylum spec.

2 juveniles. Table Bay, 33° 52' S.; 18° 28' E. Dredge, 15 m. Oct. 25, 1946. (U.C.T. Ecol. Survey TB.224.A.)

Family NYMPHONIDAE

Genus *NYMPHON* Fabr.

Nymphon modestum n. sp. Figure 3

1 specimen, holotype (probably of the female sex). Lambert's Bay, 32° 04' S.; 18° 17' E. Dredge, 23 m., rock and mussels. Jan. 22, 1957. (U.C.T. Ecol. Survey LAM.47.H.)

Description: Trunk and lateral processes smooth. Eye tubercle truncated, low; eyes well pigmented. Bases of ovigers in contact with the first pair of lateral processes. Neck not very long. Lateral processes separated by slightly less than their own diameter. Abdomen reaching to the distal end of coxa 1 of leg 4.

Chelifer scape about as long as the neck. Chelae slender, distinctly longer than the scape. Fingers longer than the palm. Movable finger with about 27, immovable finger with about 23, small teeth of similar size.

Palp segment 2 the longest; segment 5 about twice as long as segment 4. Segment 3 remarkably short, about as long as segment 5.

Distal oviger segments with very few compound spines: $6+5+3+5=19$. The compound spines bear 3 to 5 pairs of denticulations. The terminal claw bears 7 teeth.

Legs rather spinose. Tibia 2 the longer joint. Propodus about 2.5 times as long as the tarsus. Propodal sole armed with 2 shorter spines, followed by a longer one, and distally with some short spinules. Auxiliary claws about half as long as the claw.

Remarks: This species resembles *Nymphon rubrum* Hodge from the Northern Hemisphere. It has, however, much more slender chelae and a much lower number of

compound oviger spines. The closest relatives in South African waters are *N. setimanus* Brnrd. and *N. crenatiunguis* Brnrd., which both differ from *modestus* in the structure of the terminal oviger claw and in the configuration of the chelae.

This animal is modest in size, as well as in its morphological attire. It is one of the numerous forms belonging to the *grossipes*-group of the genus, though the chelae appear to be slightly more slender than usual in this group.

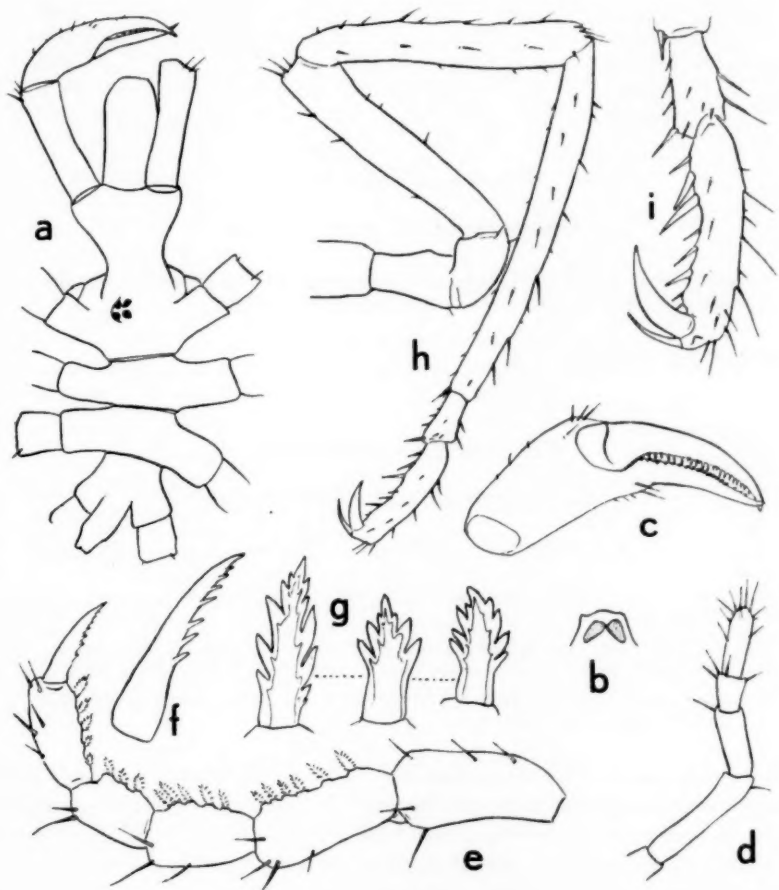


FIG. 3. *Nymphon modestum* n. sp., holotype

a, trunk in dorsal view; b, front view of eye tubercle; c, chela; d, palp; e, distal part of the oviger; f, terminal oviger claw; g, various types of compound oviger spines; h, second leg; i, distal segments of second leg.

Measurements of the holotype

	mm.
Length of trunk (frontal margin cephalic segment to tip of abdomen)	2.0
Width across the 2nd lateral processes	1.06
Length of proboscis (in dorsal view)	0.62
Second leg, coxa 1	0.33
coxa 2	0.48
coxa 3	0.33
femur	1.32
tibia 1	1.50
tibia 2	2.02
tarsus	0.26
propodus	0.66

Nymphon phasmatodes Böhm*Nymphon phasmatodes*, Stock, 1956, 76

2 females. 34° 18' S.; 18° 30' E. Dredge, 51 m. Bottom: sand, broken shells and *Phyllochaetopterus*. March 27, 1957. (U.C.T. Ecol. Survey TRA.143.X.)

An uncommon species.

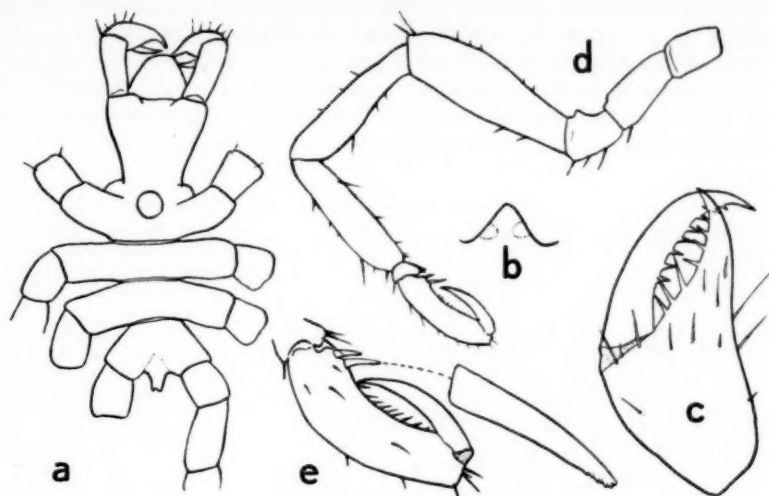
Family CALLIPALLENIDAE

Genus *PROPALLENE* Schimkewitsch*Propallene similis* Barnard. Figure 4*Propallene similis*, Barnard, 1955, 105

1 female. Mossel Bay. Dredged off Seal Island (34° 09' S.; 22° 7-10' E.), 10 m. Bottom: sand, broken shell, and rocky patches. Jan. 12, 1956. (U.C.T. Ecol. Survey MB.4.T.)

1 juvenile. Mossel Bay. 34° 10-42' S.; 22° 09' E. Dredge, 9 m., rock. Jan. 17, 1956. (U.C.T. Ecol. Survey MB.57.R.)

Remarks: This species was recently described by Barnard (1955) from a single male. However, the identification of the present material is subject to reservation, since the generic distinction in the family *Callipallenidae* is based exclusively on characters of the males. A solitary female specimen, as in this case, cannot be attributed with certainty to any particular genus. The armature of the fingers of the chelae of the present female and the type of *P. similis* are, however, in such a perfect agreement with one another that I hardly doubt the correctness of the identification. Apart from the armature of the fingers of the chelae, the present species is, as Barnard emphasized, very similar to *P. kempfi* (Calman).

FIG. 4. *Propallene similis* Barnard. ♀.

a, trunk in dorsal view; b, eye tubercle in front view; c, chela; d, third leg; e, distal segments of third leg.

Measurements of the female

	mm.
Length of trunk (frontal margin cephalic segment to tip of abdomen)	1.76
Length of cephalic segment	0.81
Width across the 2nd lateral processes	1.06
Third leg, coxa 1	0.38
coxa 2	0.49
coxa 3	0.30
femur	1.13
tibia 1	0.87
tibia 2	0.90
tarsus	0.09
propodus	0.63

Propallene crassimanus n. sp. Figure 5

1 male, holotype. Lambert's Bay, 32° 04.5' S.; 18° 18.3' E. Dredge, 17 m., sand and rock. Jan. 16, 1957. (U.C.T. Ecol. Survey LAM.2.Z.)

Description: The type specimen is rather badly damaged (all appendages on one side were lacking). Its morphology is so interesting and its distinction from the other species of the genus so easy, that I have ventured to base a new species on it.

The general aspect offers no peculiarities. The chela has 8 teeth on the movable and 2 spine-like teeth and 4 to 6 smaller teeth on the immovable finger. The palp bears a very indistinct, non-functional segmentation line at about one-third of the

length of the long segment. Oviger damaged (segment 10 lacking). Segment 5 with 2 distal lobes (as in *P. similis* Brnrd.). Spine-formula of the 7th-9th segment 14:12:12.

Femur bearing on the ventral side 13 short tubes (indicated by arrows in figure 5*f*), which probably represent the cement gland apertures. Propodus very robust. Two big spines, which are indistinctly crenulated, on the propodal heel. At the base of the claw a curious rectangular expansion. No auxiliary claws.

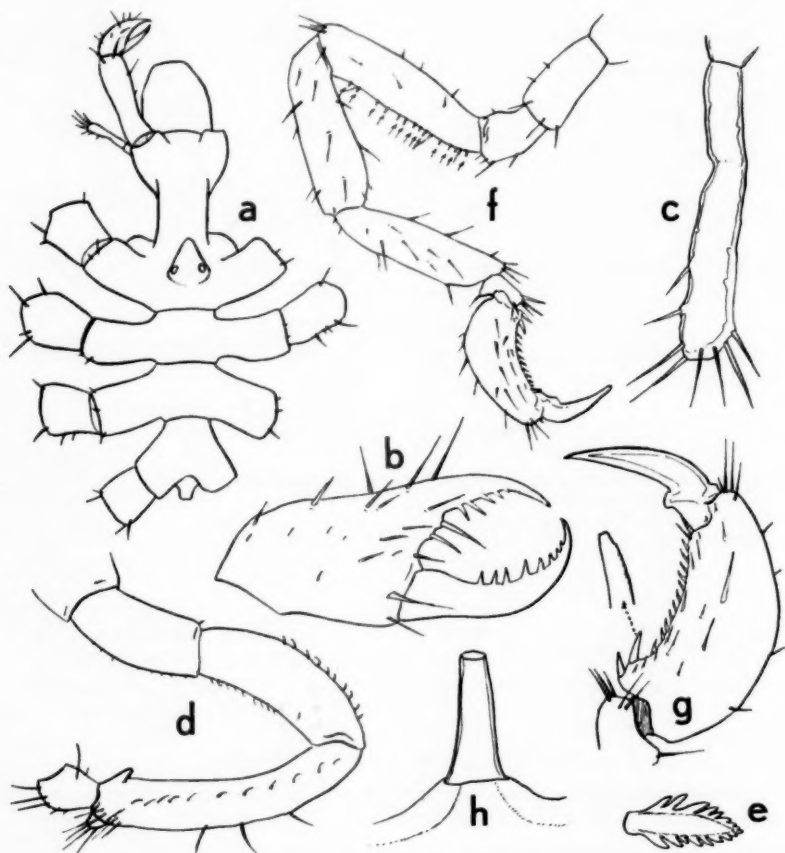


FIG. 5. *Propallene crassimanus* n. sp. ♂, holotype.

a, trunk in dorsal view; *b*, chela; *c*, palp; *d*, proximal part of oviger; *e*, compound spine from oviger segment 7; *f*, third leg (the arrows indicate the cement gland ducts); *g*, distal segments of third leg; *h*, cement gland duct.

Remarks: The very heavy propodus is distinctive. The other species of *Propallene* (*longiceps* (Böhm), *kempi* (Calman), *similis* Barnard, *stocki* Fage) have a slender propodus. In none of these species have cement gland tubes been described. Throughout the Pycnogonida, an analogous cement gland, opening through many ducts, is exceedingly rare.

Measurements of the male, holotype

	mm.
Length (frontal margin cephalic segment to tip of abdomen)	2.1
Length of cephalic segment	1.0
Length of proboscis (in dorsal view)	0.48
Width across 2nd lateral processes	1.1
Third leg, coxa 1	0.33
coxa 2	0.57
coxa 3	0.33
femur	1.06
tibia 1	0.97
tibia 2	0.92
tarsus	0.15
propodus	0.70

Genus *PALLENOPSIS* Wilson

Pallenopsis intermedia Flynn

Pallenopsis intermedia, Barnard, 1954, 117

- 2 males. 34° 19.6' S.; 18° 30.5' E. Dredge, 55 m. Bottom: sand, shells, carpets of *Phyllochaetopterus socialis*. Feb. 1957. (U.C.T. Ecol. Survey TRA.131.I.)
- 3 specimens. 34° 40' S.; 21° 35' E. Dredge, 70-77 m., rock and sponges. Nov. 28, 1952. (U.C.T. Ecol. Survey TRA.54.A.)
- 2 males, 1 female. 34° 30' S.; 20° 57' E. Trawl, 73 m., mud and stones. July 1950. (U.C.T. Ecol. Survey TRA.40.G-H.)
- 1 male, 1 female. 34° 30' S.; 20° 57' E. Trawl, 35 fathoms, in hydroids. July 1951. (U.C.T. Ecol. Survey TRA.42.J.)
- 1 male. Dredged by commercial trawler near Mossel Bay. March 1956. (U.C.T. Ecol. Survey TRA.101.A.)

Genus *HANNONIA* Hoek

Hannonia typica Hoek

Hannonia typica, Barnard, 1954, 123

South West Africa

- 1 ovigerous male. Lüderitz, shore collection. July 1957. (U.C.T. Ecol. Survey SWA.5.U.)

Langebaan Lagoon (33° 05' S.; 17° 55' E.)

- (a) 1 female. Oosterwal. Collected by hand on sand banks at low tide. Dec. 12, 1950. (U.C.T. Ecol. Survey LB.218.L.)
- (b) 1 ovigerous male. Botlary, on *Zostera* flat at M.S.L. Dec. 5, 1953. (U.C.T. Ecol. Survey LB.403.E.)
- (c) 1 female. Dredging Langebaan Lagoon, 3-4 m. Sand and shell. May 6, 1955. (U.C.T. Ecol. Survey LB.472.F.)

? *Hannonia* spec. Figure 6

- (a) 1 postlarval juvenile. Saldanha Bay, 33° 03' S.; 17° 58-5' E. Dredge, 7 m., sandy limestone bored by *Polydora*. July 13, 1946. (U.C.T. Ecol. Survey SB.117.B.)
 (b) 1 postlarval juvenile. Langebaan Lagoon, 33° 05' S.; 17° 55' E. On mudbank, parasitic on *Audouinia australis* (Polychaeta). April 29, 1956. (U.C.T. Ecol. Survey LB.491.A.)

Remarks: Figure 6 illustrates this very remarkable case of a pycnogon parasitic on a polychaet. Except for some more or less vague indications (cf. Helfer & Schlottke, 1935, 200) this is the first instance in which a polychaet host is recorded.

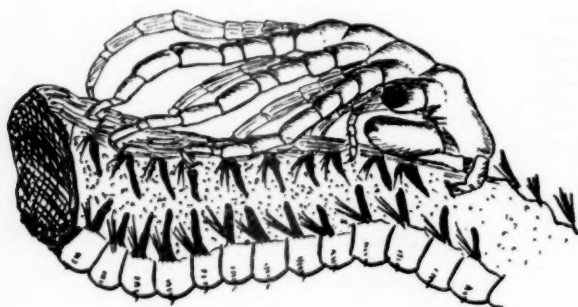


FIG. 6

? *Hannonia* spec. A postlarval juvenile, parasitic on the polychaet *Audouinia australis*. Freehand sketch.

Genus *QUEUBUS* Barnard*Queubus jamesanus* Barnard. Figure 7

Queubus jamesanus Barnard, 1946, 63; 1954, 157; 1955, 107

1 female. Saldanha Bay, 33° 05' S.; 17° 55' E. Lynch Point. Shore, from pools under granite boulders. Sept. 22, 1957. (U.C.T. Ecol. Survey SB.154.G-H.)

Remarks: This curious genus was established by Barnard on a single male specimen found at St. James, False Bay. As he remarked, the 'absence of the ♀ makes the position and the relationships of the genus uncertain'. In 1955 he recorded two further specimens, the sex of which was not noted.

The present collection contained one more specimen referable to the genus, and it proved to be a female.

The genital pores are large, present on the ventral surface of the 2nd coxae of all legs. In its general morphology the female closely resembles the male. The sub-chelate shape of the propodus is less clearly defined than in Barnard's illustration of

the holotype. The mid-dorsal bosses on the trunk are lower, and there is less space between the lateral processes. The ovigers of both sexes are very similar, the female seems to lack the bifid spine on the 6th segment.

The female is 3.0 mm. long (frontal margin cephalic segment to tip of abdomen); the proboscis is 2.3 mm. long.

The genus shows a certain resemblance to the genera *Pallenopsis*, *Pigrogromitus*, and *Hannonia*, and certainly belongs to the same family as these.

Family PHOXICHILIDIIDAE (incl. Endeidae)

Genus *ENDEIS* Philippi

Endeis clipeatus (Möbius)

Endeis clipeatus, Barnard, 1954, 129

- (a) 1 male. Table Bay, 33° 52' S.; 18° 28' E. Dredge, 15 m. Oct. 25, 1946. (U.C.T. Ecol. Survey TB.224.A.)
- (b) 1 female. 34° 40' S.; 21° 35' E. Dredge, 70-77 m., rock and sponges. (U.C.T. Ecol. Survey TRA.56.Z.)
- (c) 1 juvenile, probably this species. 34° 18.2' S.; 18° 30.6' E. Dredge, 51 m. Bottom: sand, shell, and carpets of *Phyllochaetopterus socialis*. March 27, 1957. (U.C.T. Ecol. Survey TRA.142.U.)
- (d) 1 specimen. Natal, shore collection from Imbotje (31° S.; 29° E.). Below L.W.S. July 13, 1956. (U.C.T. Ecol. Survey NA.194.Y.)

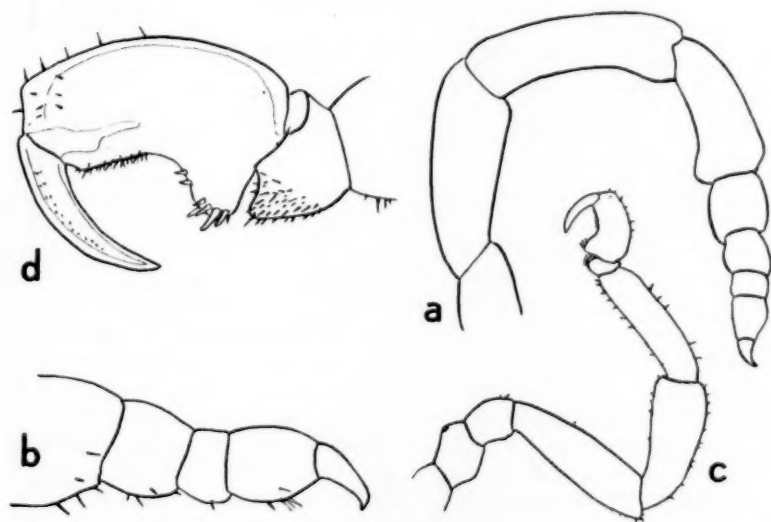


FIG. 7. *Queubus jamesanus* Barnard. ♀.

a, oviger; b, distal oviger segments; c, second leg; d, distal segments of second leg.

Genus *ANOPLODACTYLUS* Wilson*Anoplodactylus unilobus* n. sp. Figure 8

1 female, holotype. Table Bay, off Chapman's Peak (34° 5' S.; 18° 20' E.). Dredge, 11 m., sand. (U.C.T. Ecol. Survey TB.237.A.). Sept. 15, 1949.

Description: Neck distinct. The base of the neck is widened (rudiment of the oviger-bases?). Lateral processes well separated. Trunk segmented, but the intersegmental line between segments 3 and 4 is feebly developed. Abdomen erect. Eyes present. Proboscis with an unpaired, rounded projection in the median line of its ventral surface.

Chelifer scape curved outwards. Chelae with smooth fingers. No palps, no ovigers.

Legs relatively long. A strong process, bearing the female genital pore on its tip, is present on the ventro-distal corner of the second coxae of all legs. Legs nearly smooth. Propodus with a strong heel bearing 2 strong and 5-6 smaller spines.

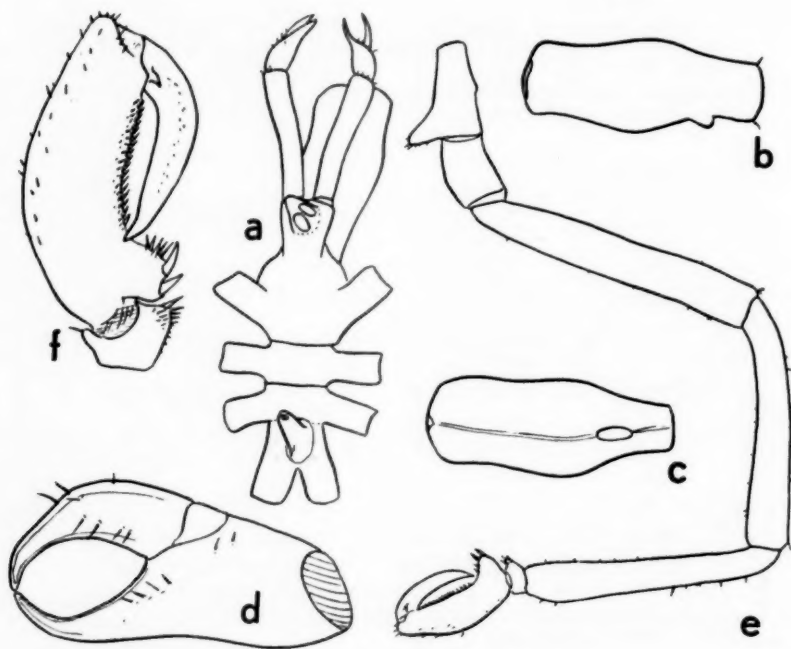


FIG. 8. *Anoplodactylus unilobus* n. sp. ♀, holotype.

a, trunk in dorsal view; b, proboscis from the left; c, proboscis in ventral view; d, chela; e, second leg; f, distal segments of second leg.

Propodal sole with several rows of spinules; the main row with about 17 spinules. Rudimentary auxiliary claws present.

Remarks: Superficially closely resembling *Phoxichilidium capense* Flynn. The new species has, however, the neck more strongly developed. *P. capense* has the trunk completely and distinctly segmented, *A. unilobus* lacks a distinct articulation between trunk segments 3 and 4. The armature of the propodal sole is another easy character to distinguish *A. unilobus* from *P. capense*. The *unpaired* ventral outgrowth of the proboscis separates *A. unilobus* at once from all other members of the genera *Phoxichilidium* and *Anoplodactylus* (*paired* outgrowths exist in a number of species).

I am aware that Utinomi (1955) synonymized the genus *Anoplodactylus* with *Phoxichilidium*, but (though agreeing with most of his arguments) I retain the generic name *Anoplodactylus* for the moment, as a matter of convenience and for lack of a better one.

Measurements of the female holotype

	mm.
Length (frontal margin cephalic segment to tip of 4th lateral process)	4.1
Width across the 2nd lateral processes	2.3
Second leg, coxa 2	1.2
coxa 3	0.98
femur	3.8
tibia 1	3.4
tibia 2	3.4
propodus	1.7

Family PYCNOGONIDAE

Genus *PYCNOGONUM* Brünnich

Pycnogonum angulirostrum n. sp. Figure 9

1 female, holotype. False Bay, Dalebrook. Collected by hand at M.S.L. under stone in pool. Sept. 17, 1955. (U.C.T. Ecol. Survey CP.439.S.)

Description: Trunk completely segmented. Ocular tubercle low, truncated, eyes not very distinctly pigmented. At the posterior half, in the median line of each of trunk segments 1, 2, and 3, a big disc-shaped prominence occurs. Between the eye tubercle and the big prominence on the cephalic segment there is a smaller tubercle. Distal ends of the lateral processes with slight elevations, those on the 4th pair of lateral processes being the largest. The entire integument of the dorsal surface of the trunk, of the dorsal prominences, of the dorsal side of the proboscis, and of certain parts of the legs, is covered with minute rugosities and tubercles.

Proboscis shows at about one-third of its length 4 expansions (2 dorso-lateral, and 2 lateral), which give it an angular appearance. A large dermal fold at the base of the proboscis. Abdomen spatulate, truncated at the distal end.

Legs with numerous small tubercles and rugosities, particularly on the femur and the tibiae. Femur with a strong ventral hump. Tarsus on the ventral side with a shining patch, bearing numerous stiff spinules. No auxiliary claws. Genital pores (♀) on the dorsal surface of the 2nd coxae of the last pair of legs.

Remarks: The species shows resemblances to *Pycnogonum aurilineatum* Flynn (1919) from Tasmania, but it differs from this and from all other species of the genus in the curious structure of the proboscis.

Measurements of the holotype

	mm.
Length (tip of proboscis to tip of abdomen)	7.3
Length of proboscis (in dorsal view)	1.9
Width across the 2nd lateral processes	2.7
Third leg, coxa 1	0.61
coxa 2	0.53
coxa 3	0.44
femur	0.97
tibia 1	1.01
tibia 2	0.61
tarsus + propodus	0.88

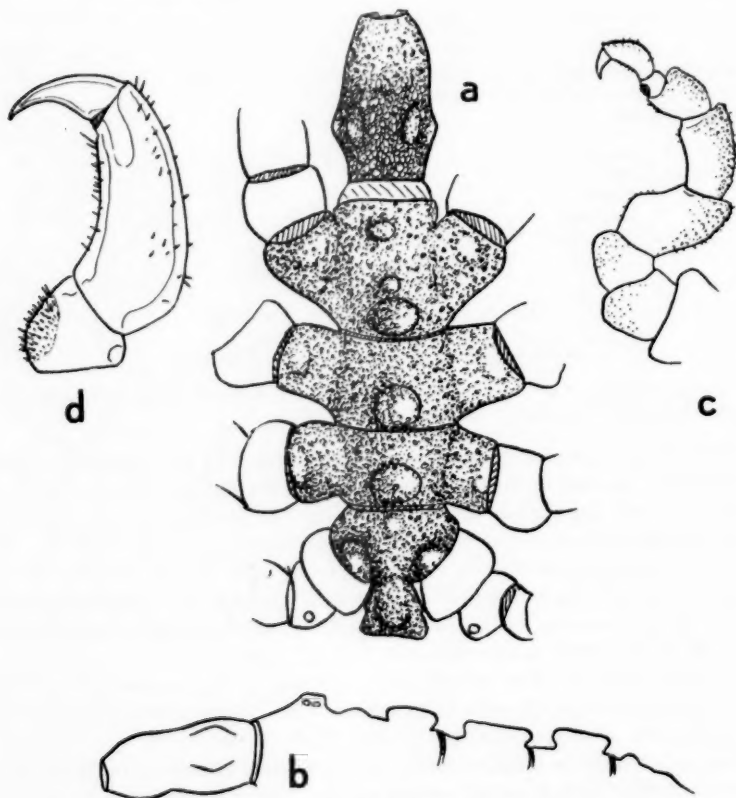


FIG. 9. *Pycnogonum angulirostre* n. sp. ♀, holotype.

a, trunk in dorsal view; b, contour of the dorsum; c, third leg; d, distal segments of third leg.

REFERENCES

A nearly complete bibliography of pycnogonid literature is to be found in the papers of Helfer and Schlottke (1935), Hedgpeth (1947), and Stock (1956). The only paper not mentioned in these bibliographies is that of Barnard (1955).

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NEW MITE PARASITES FROM SOUTH AFRICAN LIZARDS AND BATS

By R. F. LAWRENCE

(Natal Museum, Pietermaritzburg)

(With three text-figures)

(Read August 20, 1958)

Two new species of scale-mites (Pterygosomidae) are described from lizard hosts, and the male of a third species, previously known from females only. A new Listrophorid mite, from the Cape Horseshoe bat, is also described.

The Acarine parasites of South African lizards and bats have been systematically studied during recent years and can now be said to be fairly well known. Both groups of animals harbour a mite fauna belonging to three quite separate groups of Acarina: the Trombidiformes, Sarcoptiformes and Mesostigmata. In the following pages some new or little-known species belonging to the two first-named groups are described. My thanks are due to Dr. F. Zumpt of the South African Institute for Medical Research, Johannesburg, who collected most of them.

TROMBIDIFORMES

Family PTERYGOSOMIDAE

Genus *PTERYGOSOMA* Peters

Pterygosoma rubicundum n. sp.

Figure 1 (a-f)

Types. 5 ♂♂, 2 ♀♀, from belly scales of *Agama armata armata*, Mt. Gorongosa near Vila Paiva, Portuguese East Africa (NM. 6576), collected by R. F. Lawrence, Sept. 1957.

Colour. Body bright red.

♀. *Dorsal surface* as in fig. 1(a), the number of peripheral hairs on each side 25-34 (average of 31 in a count of 5 specimens), their shafts with a small part of the apex flattened and roughened with fine spicules, except in 1 or 2 which are pointed apically. Anal field as in fig. 1(c), enlarged, the group of two anterior hairs flattened, paddle-shaped, the anterior of these definitely shorter but wider than the other pair which is the longest of all the anal hairs; the posterior group consisting of two oblique

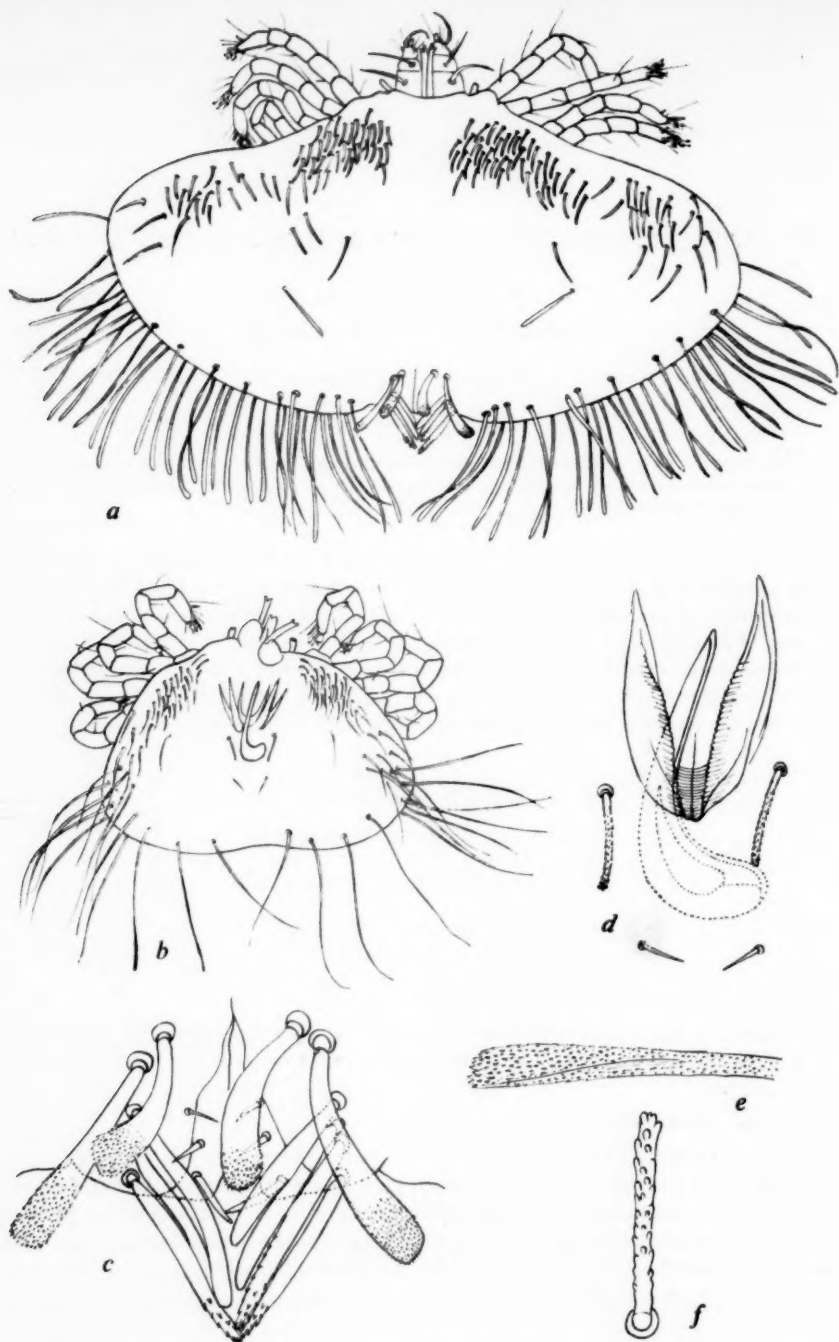


FIG. 1. *Pterygosoma rubicundum* n. sp. (a) dorsal surface of ♀; (b) of ♂; (c) anal field of ♀ enlarged; (d) genitalia of ♂ enlarged; (e) apex of peripheral pair of ♀ enlarged; (f) scapular hair of dorsum of ♀.

rows of 3 or 4 more or less cylindrical hairs, their apices spiculate; mesially to this row 3 smooth spines on each side, the posterior longest and thickest.

Ventral surface. A pair of widely separated fairly long spiniform setae above the level of the anal field, another on each side halfway between this and the lateral apex of the body (this pair with minute spicules); a third pair anterior to the first-named genital pair, forming with them a quadrilateral wider in front than behind.

♂. *Dorsal surface* as in fig. 1(b) with long, sinuous, pointed hairs not barbed or spiculated; opening for penis situated dorso-anteriorly not far behind the insertion of chelicerae, V-shaped, the penis itself pistol-shaped, figs. 1(b), (d); in the type, fig. 1(b), the base of the penis has been pressed forward and bent in mounting but fig. 1(d) of another male with an undistorted penis represents more accurately the actual shape of the organ. The posterior half of the penis covered by transparent skin, the front half seen emerging from the V-shaped genital aperture. The shape of the penis and position of the genital aperture on the dorsal surface resemble those described and figured by Lavoipierre for *P. crewei* (1955, p. 123, fig. 2).

Dimensions. Female, length of body 800μ , width $1,200\mu$; male, length of body 460μ , width 600μ .

The species resembles *aculeatum* Lawrence (1936) most closely in the number of peripheral hairs, which are, however, fewer and more spatulate at their tips; it has about the same number of hairs as *triangulare* Lawrence (1936) but these are not pointed at the sides and the group of posterior genital hairs are much shorter (in *triangulare* the posterior hairs are twice as long as the anterior); finally it resembles *agamae* Peters (1849) in having nearly all the peripheral hairs spatulate, differing from it in the shape of the genital hairs.

Pterygosoma (Gerrhosaurobia) gerrhosauri Lawrence

Figure 2(b-g)

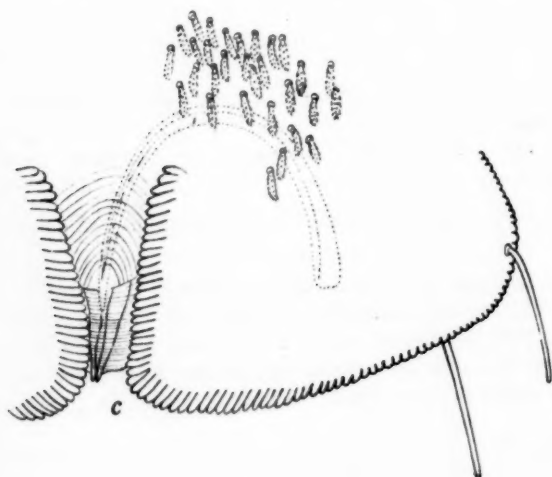
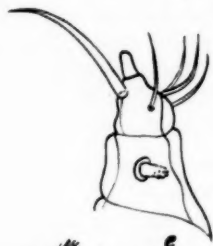
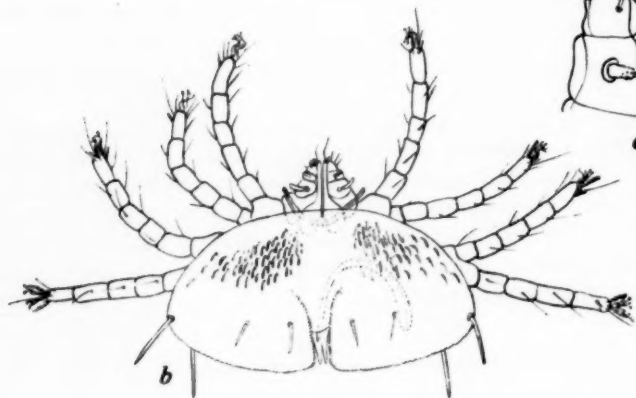
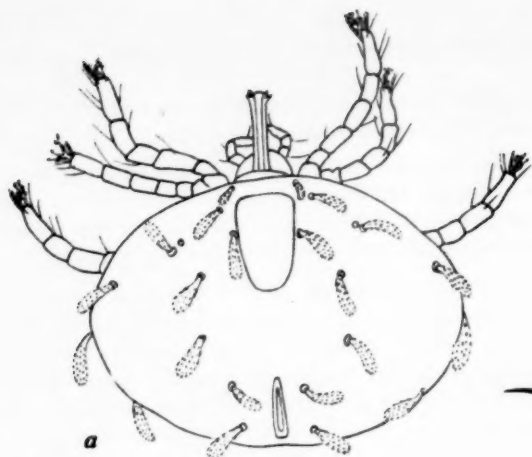
P. gerrhosauri Lawrence 1935, *Parasitology*, 27(1), p. 33, fig. 19.

1 ♂, 1 ♀ from *Gerrhosaurus validus*, Gravelotte, eastern Transvaal, collected by F. Zumpt, Oct. 1957.

The female type was taken from the same host, Zululand; the following is a description of the male.

♂. *Colour.* The body half filled with blackish material, otherwise yellowish or transparent.

Dorsal surface as in fig. 2(b), the penis, seen through the transparent skin of the dorsal surface, very long and relatively very large, curved in a semicircle with the pointed apex directed posteriorly, its distal half lying in a well-defined wide but shallow groove, fig. 2(c), near the external opening of this groove a sheath or adeagus composed of two valves between which the shaft of the penis is apparently extruded.



Ventral surface with 2 or 3 pairs of short setae or rod-like hairs, the exact number obscure. Mouth-parts as in the ♀, described below.

♀. The group of scapular hairs of much the same size and shape as in the ♂, fig. 2(g), fairly broad and lanceolate, differing from those of *Pterygosoma* species (*sens. strict.*) which are rod-like, almost truncate, and of even width throughout their length, fig. (f); hypostome differing from typical *Pterygosoma* in having a curved row of 4 minute teeth on each side of its apex, fig. 2(f), while in species from Agamid lizards it is usually a simple plate with or without a weak incision in the middle. Pedipalp as in fig. 2(d), seen from below, the basal and second segments with a stout, blunt, roughened hair, that of the second distinctly shorter than that of the basal segment; the two apical segments with setation as in fig. 2(e), seen from above.

Dimensions. Male, length of body 316μ , width 460μ ; female, length of body 500μ , width 840μ . In the original description of the female type, the body length was erroneously given as 0.8 mm., the breadth as 0.4 mm., instead of vice versa.

As pointed out by Lavoipierre (1955, p. 122) there are distinct differences between those species of *Pterygosoma* which parasitize Gerrhosauridae and those living on Agamidae, one of them, as he has observed, being the fact that the penis of the ♂ is directed forwards in the latter, backwards in the former; in the males of all three species from Gerrhosaurids that have now been described and the two from Agamidae, this distinction holds good and can be taken as a reliable generic character in the males. I therefore propose the subgeneric name *Gerrhosaurobia* for distinguishing the mites of the family Pterygosomidae which parasitize Gerrhosaurid lizards. The type species for the subgenus would be *Pterygosoma validus* Lawrence.

While recognizing the fairly close general relationship of scale-mites in these two unrelated families of lizards, the generic or subgeneric characters separating them can be tabulated as follows:

Subgenus *Gerrhosaurobia*

1. Scapular hairs lanceolate, fairly wide.
2. Anal field situated on ventral surface.
3. Genital field with a row of similar hairs.
4. Apex of hypostome with minute teeth.
5. Penultimate segment of pedipalp with a short, thick, blunt-tipped hair.
6. Penis of ♂ directed backwards.

Subgenus *Pterygosoma*

- Scapular hairs bacilliform, of even width throughout.
- Anal field on dorsal surface.
- Genital field with some of the hairs differentiated, flattened or rounded.
- Apex of hypostome not toothed.
- Penultimate segment of pedipalp with a long tapering seta.
- Penis of ♂ directed forwards.

FIG. 2. *Zonurobia debilipes mossambica* n. subsp. (a) dorsum of larva. *Gerrhosaurobia gerrhosauri* (Lawr.); (b) dorsum of ♂; (c) genito-anal region enlarged; (d), (e) ventral and dorsal apices of ♀ pedipalp; (f) hypostome of ♂; (g) scapular hair of ♂ enlarged.

Genus *ZONUROBIA* Lawrence*Zonurobia debilipes mossambica* n. subsp.

Figure 2(a)

Types. 30 ♀♀ (NM. 6575) and 12 larvae (NM. 6594) from *Cordylus warreni mossambicus* FitzSimons, a new subspecies of Cordylid lizard from Mt. Gorongosa, near Vila Paiva, Portuguese East Africa; collected by R. F. Lawrence, Oct. 1957.

♀. These specimens agree well with *debilipes* Lawrence (1935), hitherto known only from *Cordylus warreni warreni*, in the arrangement and shape of the hairs. They differ only in the greater length of the body in relation to its width, the ratio being 0.71 in the above variety, 0.59 in typical *debilipes*, taking an average of measurements of 7 unmounted specimens for each. In typical *debilipes* the body is slightly more quadratiform, in *debilipes mossambica* a little more rounded.

Dimensions. Length of body, 1.02 mm., width 1.44 mm. (largest female); of smallest ♀, 0.72 mm. and 1.1 mm. respectively.

Larva. Dorsal surface as in fig. 2(a), with 10 or 11 pairs of flattened club-shaped spiculated hairs; eyes very small, not much larger than a hair socket, situated about midway between the elongated dorsal scute and sides of body. Ventral surface with anal opening consisting of a median slit near posterior margin of body, its posterior end flanked on each side by two flattened hairs, the posterior one wider, both similar to those of the dorsal surface, ventral surface otherwise without setation except for a pair of setae below the mouth parts. In the dorsal scute and structure of the dorsal hairs it resembles the larva of *Ixodiderma inverta* (Lawrence, 1951, p. 450, fig. 3).

Dimensions. Length of body, 0.250 mm., width 0.340 mm.

SARCOPTIFORMES

Family LISTROPHORIDAE

Genus *ALABIDOCARPUS* Lawrence*Alabidocarpus diceratops* n. sp.

, Figure 3(a), (b)

Types. 2 ♀♀ from *Rhinolophus capensis*, Table Mt., Cape Town, collected by F. Zumpt, Sept., 1957.

Colour as in all other species of the genus.

♂. *Body.* Apical section of anterior dorsal shield separate from the basal portion and strongly chitinized, ending posteriorly in two equal-sized, strong, horn-like processes, directed backwards, fig. 3(a), dorsal shield sharply pointed posteriorly, as in *Alabidocarpus nasicolus*, shaped almost in the form of a wide isosceles triangle; three minute spines along the posterior margin of shield, the most ventral opposite its posterior apex; the large lateral seta above the insertion of leg III unusually short

and very thick, especially basally, just below and a little anterior to it an extremely minute short seta. Body with ± 75 annulations, a pair of unusually stout and moderately long setae at its posterior apex, below these a minute pair.

Legs. Epimera of leg IV without either a pair of short lanceolate spines as in *calcaratus*, or long setiform ones as in *nasicolus*; claws of tarsi III and IV only slightly curved as in *calcaratus*, spur of leg IV a third length of claw, of III two-fifths.

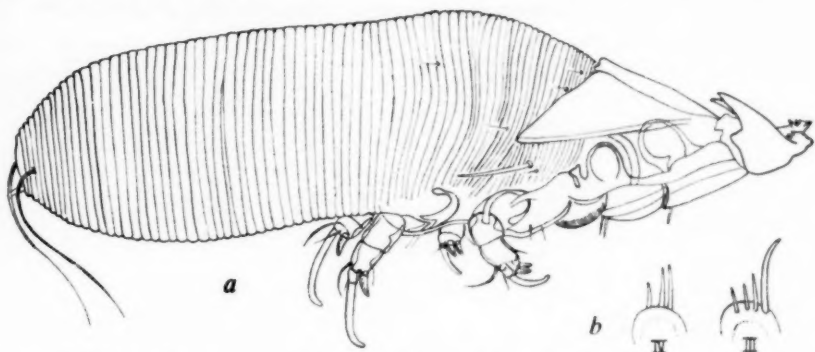


FIG. 3. *Alabidocarpus diceratops* n. sp. (a) ♀ in lateral view; (b) the rudimentary third and fourth legs of nymph.

Nymph equal in length to the female but considerably deeper (280μ as compared with 174μ), with about 60 annulations, in general resembling the nymph of *calcaratus* (1952, p. 139, fig. 1(b)), the papilla representing leg III, however, crowned with 4 spines, fig. 3(b), longer than those of IV which appear to be only 3 in number, though these cannot be so clearly seen as in III; papillae representing legs I and II apparently with 2 spines each but these are also obscure.

Dimensions. Body length of female and nymph 600μ ; depth of ♀ 174μ , of nymph 280μ .

The three South African species can be distinguished by the following key:

- | | |
|--|----------------------------|
| 1. Body with 75 annulations, apex of dorsal anterior shield with two large horn-like processes | <i>diceratops</i> n. sp. |
| Body with 60 annulations, apex of dorsal anterior shield without large horn-like processes | 2. |
| 2. Epimera of leg IV with a pair of lanceolate spines resembling the tarsal spurs; posterior margin of dorsal shield rounded or truncate . . . | <i>calcaratus</i> Lawrence |
| Epimera of leg IV with a pair of long setiform spines; posterior margin of dorsal shield sharply angular | <i>nasicolus</i> Lawrence |

Genus *LABIDOCARPUS* Trouess.

Labidocarpus natalensis Lawrence

A number of females from *Rhinolophus capensis*, Table Mt., Cape Town, collected by F. Zumpt, Sept., 1957.

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THE UNIVERSITY OF CHICAGO
DIVISION OF THE PHYSICAL SCIENCES
DEPARTMENT OF CHEMISTRY
CHICAGO, ILLINOIS 60637

TO THE EDITOR OF THE JOURNAL OF THE AMERICAN CHEMICAL SOCIETY
FROM THE DEPARTMENT OF CHEMISTRY, UNIVERSITY OF CHICAGO
CHICAGO, ILLINOIS 60637
U.S.A.
Dear Sir,
I have the honor to acknowledge the receipt of your letter of the 10th inst. in relation to the paper of mine and my colleagues, entitled "The Structure of the Benzene Ring," published in the JOURNAL OF THE AMERICAN CHEMICAL SOCIETY, Vol. 78, No. 1, p. 1, 1956.
The paper in question is a review of the literature on the structure of the benzene ring, and is not a report of original research. It is, therefore, not subject to the same standards of review as original research papers. I am, however, glad to hear that it has been found useful by you and your colleagues.
Very respectfully,
R. M. MARZULLI
Professor of Chemistry
University of Chicago
Chicago, Illinois 60637

THE HISTORY OF THE CITY OF BOSTON

FROM 1630 TO 1800

By JOHN H. COLEMAN, Esq. of the City of Boston.
Published by J. B. LEECH, at the City of Boston.
1800.

TRANSACTIONS OF THE ROYAL SOCIETY OF SOUTH AFRICA

Volume XXXV

MINUTES OF PROCEEDINGS, 1955

COUNCIL FOR 1955

President: S. H. Haughton, D.Sc.

Hon. General Secretary: W. J. Talbot; *Hon. Treasurer:* N. Sapeika; *Acting Hon. Editor of Transactions:* A. M. Talbot; *Hon. Librarian:* E. Newbery; *Other Members of Council:* H. B. S. Cooke, W. J. Copenhagen, J. H. Day, R. Elsdon-Dew, C. v. Riet Lowe, S. M. Naudé, S. H. Skaife, J. B. L. Smith.

REPORT OF THE HONORARY GENERAL SECRETARY FOR 1955

The Anniversary Meeting, the Annual Meeting, and six Ordinary Meetings of the Society were held at the Athenaeum, 154 Camp Ground Road, Newlands; the Ordinary Meetings in September and November were held at the University Medical School, Mowbray.

The Presidential Address, 'The Argentine Ant', was delivered by the retiring President, Dr. S. H. Skaife, at the March meeting. Others papers read during the year were:

1. 'The subterranean mammals of the world', by J. R. Ellerman. September 21.
2. 'The surface geology of the Hopefield Fossil Site', by J. A. Mabbutt. September 21.
3. 'The hand- and foot-form of the Koranna', by C. S. Grobbelaar. November 16.

Six lectures were given before the Society:

1. 'The blood-grouping and physical characteristics of the Koranna', by C. S. Grobbelaar. April 20.
2. 'Viruses as tools in the study of genetics', by M. van den Ende. May 18.
3. 'The work of the Fisheries Research Institute', by G. M. Dreosti. June 15.
4. 'The elusive neutrino', by A. M. Cormack. August 17.
5. 'The Royal Institution', by Sir Lawrence Bragg. September 21.
6. 'Plant gums: their structure in relation to their origin', by A. M. Stephen. October 19.

At the November meeting, a discussion of J. A. Mabbutt's paper (read by title only in September) introduced a symposium on the Hopefield Fossil Site in which M. R. Drennan, K. Jolly, E. N. Keen and R. Singer discussed the nature and significance of the discoveries.

At the Annual Meeting the following were elected to Fellowship:

ANTON LINDER HALES, M.Sc., Ph.D. (CAPE TOWN), M.A. (CAMBRIDGE)

in recognition of outstanding research in geophysics.

JULIUS STAZ, D.D.S. (RAND), H.D.D. (GLASGOW), L.D.S. (ENG.)

in recognition of outstanding research in odontology.

The deaths of Dr. T. B. Davie, a Fellow of the Society since 1948, Dr. A. L. Hall, a Fellow since 1909, Professor W. Pugh, a Fellow since 1934, Dr. H. R. Raikes, a Fellow since 1938, and Dr. L. B. Goldschmidt, a Member since 1924, are recorded with the deepest regret.

At the end of 1955 the number of Fellows was 91 and there were 190 Members, including six new Members elected during the year.

The Council wishes to express the thanks of the Society to the Department of Education, Arts and Science for a grant of £400, to the University of the Witwatersrand for a grant of £23 3s. 8d, and to Messrs. de Beers Consolidated Mines Ltd. for a grant of £10 10s. 0d. It is also grateful for an anonymous gift of £200 and for £7 5s. 0d. donated to the Society's general funds by various members.

Invitations were received to nominate delegates to a number of scientific congresses overseas: W. E. Isaac represented the Society at the Meetings of the British Association in September and M. R. Drennan at the Pan-African Congress on Prehistory at Livingstone in July 1955.

The exchange mailing list was revised during the year, leaving 211 institutions (including 25 institutional members) on the list at the end of 1955.

From the Society's library 211 periodicals and 69 books were issued during the year.

The Council gratefully acknowledges the receipt of a number of books and periodicals from various donors, including an almost complete set of the Society's own Transactions from Vol. 5, pt. 1 to Vol. 34, pt. 3 donated by R. S. Adamson.

W. J. TALBOT,
Hon. General Secretary.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR JANUARY 1, 1955, TO DECEMBER 31, 1955

EXPENDITURE		£	s.	d.	£	s.	d.
To Clerical Assistance					60	0	0
" Petty cash (Clerical Assistant)	14	12	1½				
" Petty cash (Editor & Secretary)	9	0	3				
				23	12	4½	
" Stationery				13	19	6	
" Printing				8	4	0	
" Hire of hall, La Rochelle ..				6	4	6	
" Library rent and insurance, of 1955				36	18	0	
" University Film Unit				1	1	0	
" Rustica Press: printing and distribution of Transactions (Vol. 34, pts. 1 and 2) ..	623	1	2				
Less provision, 1954	350	17	2				
				272	4	0	
" Neill & Co.				2	10	0	
" Librarian, U.C.T. (Photographing Charter) ..				1	4	11	
" Purchase of old volumes of the Transactions				1	4	1	
" Athenaeum (capitation fee for new members)				1	5	0	
" President (Entertainment of visiting lecturers) ..				3	1	0	
" Bank charges				4	8	7	
" Transfer to Reserve for Publications				700	0	0	
" Unappropriated income ..				62	5	10½	
" Interest as per contra capitalized (less £3 ls. 0d. paid ex President's Fund)				89	3	10	
				£1,287	6	8	
INCOME		£	s.	d.	£	s.	d.
By Subscriptions - 1956				9	2	0	
" - 1955				354	5	3	
" - 1954				23	5	0	
" - 1953				4	1	0	
				390	13	3	
" Entrance fees				4	0	0	
" Sale of publications and reprints							
Transactions of the Society ..	81	6	5				
Broom Commemorative Volume	3	16	3				
Wicht Report				5	3		
Reprints	74	2	0				
				159	9	11	
" Grants:							
Secretary for Education ..	400	0	0				
Anon (via Dr. Skaife)	200	0	0				
University of the Witwatersrand	23	3	8				
De Beers' Consolidated Mines Limited	10	10	0				
				633	13	8	
" Interest accrued:							
Post Office Savings Bank ..	38	6	10				
Cape of Good Hope Savings Bank	40	12	10				
Marloth Memorial Fund:							
(a) Rand Prov. Bldg. Soc. Int. F/D	4	15	2				
(b) United Bldg. Soc. Int. F/D	4	3	11				
President's Fund interest ..	4	6	1				
				92	4	10	
" Donations to General Funds ..				7	5	0	
				£1,287	6	8	

LIABILITIES AND ASSETS AT DECEMBER 31, 1955

LIABILITIES		£	s.	d.	£	s.	d.
Marloth Memorial Fund:							
Capital a/c as at 31.12.54 ..	269	5	3				
Interest, 1955	8	19	1				
				278	4	4	
Life Fund Donations a/c:							
Capital a/c as at 31.12.54 ..	1,219	16	8				
Accrued interest at Cape of Good Hope Savings Bank ..	40	12	10				
Accrued interest at Post Office Savings Bank	7	10	6				
				1,268	0	0	
President's Fund:							
Capital a/c as at 31.12.54 ..	108	3	8				
Accrued capital at United Building Society	4	6	1				
				112	9	9	
Less payment to President for entertaining	3	1	0				
				109	8	9	
Reserve for publications ..	1,400	0	0				
Reserve for binding	1,200	0	0				
				2,600	0	0	
Reserve for publication of Index to the Transactions (C.S.I.R. grant)				500	0	0	
Capital account:							
Balance at 31.12.54	107	19	0				
Accrued interest (Post Office) ..	30	16	4				
				138	15	4	
Add unappropriated income ..	62	5	10½				
				201	1	2½	
				£4,956	14	3½	
ASSETS		£	s.	d.	£	s.	d.
Post Office Savings Bank:							
Current savings account ..				1,316	12	9	
Cape of Good Hope Savings Bank:							
A/c No. 86509 (General Fund) ..				572	2	9	
A/c No. 79467 (Life Fund) ..				484	18	7	
Marloth Memorial Fund:							
Rand Prov. Bldg. Soc. F/D ..	124	12	2				
United Bldg. Soc. F/D	109	2	2				
				233	14	4	
President's Fund:							
United Bldg. Soc. F/D	104	0	0				
United Bldg. Society Savings Bank	5	8	9				
				109	8	9	
Balance at Bank 31.12.55 ..				2,216	3	3	
Cash on hand				4	0	1½	
Credit at the Rustica Press ..				19	13	9	
				£4,956	14	3½	

Note:—The above-mentioned assets do not include the value of the Library and Publications of the Society held in stock.

We hereby certify that we have examined the accounts of revenue and expenditure and of assets and liabilities, that we have compared them with the books, vouchers and other documents related thereto, and that in our opinion these accounts set forth a correct description of the affairs of the Society.

H. B. RYCROFT
MARTIN J. POLLARD } Hon. Auditors.

R. H. STOV, Acting Hon. Treasurer

TRANSACTIONS OF THE ROYAL SOCIETY OF SOUTH AFRICA
Volume XXXV

MINUTES OF PROCEEDINGS, 1956

COUNCIL FOR 1956

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REPORT OF THE HON. GENERAL SECRETARY FOR 1956

The Anniversary Meeting, the Annual Meeting, and seven Ordinary Meetings were held during the year at The Athenaeum, 154 Camp Ground Road, Newlands; the Ordinary Meeting in April was held at the University of Cape Town Medical School, Observatory.

The Presidential Address, 'Inter-state co-operation in scientific and technical research in Africa south of the Sahara', was delivered by Dr. S. H. Haughton at the April meeting.

Other communications read during the year were:

1. 'Hydrobiological Studies on the Great Berg River: Part 1', by A. D. Harrison and J. F. Elsworth. May 16.
2. 'Some South African Bryozoa', by C. H. O'Donoghue, communicated by J. H. Day. May 16.
3. 'Hydrobiological Studies on the Great Berg River: Part 2: Quantitative studies on sandy bottoms, notes on tributaries, and further information on the fauna, arranged systematically', by A. D. Harrison. August 15.
4. 'Hydrobiological Studies on the Great Berg River: Part 4: The Chironomidae', by K. M. F. Scott. August 15.
5. 'Observations on the Fish River Canyon in South West Africa', by E. S. W. Simpson and D. Hywel Davies. August 15.
6. 'Some features of the relationship between mass defect and mass number', by L. H. Ahrens. September 19.
7. 'An inclusion-bearing olivine melilitite from Mukorob, South West Africa', by J. J. Frankel. September 19.
8. 'Hydrobiological Studies on the Great Berg River: Part 3: The effects of organic pollution on the fauna of the Great Berg River and of the Krom Stream, Stellenbosch', by A. D. Harrison. November 21.

Six lectures were given before the Society:

1. 'The hand- and foot-form of the Koranna', by C. S. Grobbelaar (discussing a communication read on November 16, 1955). March 21.
2. 'The chemical effects of defects in solids', by F. Sebba. May 16.
3. 'On an expedition to the northern Transvaal to study the circulation of the Giraffe', by R. Goetz. June 20.
4. 'High-altitude vegetation', by E. A. C. L. E. Schelpe. August 15.
5. 'Development and deterioration of the higher mental processes in Man', by K. R. L. Hall. September 19.
6. 'The significance of isotope abundance distribution', by L. H. Ahrens (expanding and discussing a communication read on September 19). October 17.

At the Meeting on November 21 a symposium was held on the 'International Geophysical Year, 1957-58'. Speakers included R. H. Stoy, R. Guelke and J. H. Day.

At the Annual Meeting in October Keppel Harcourt Barnard was elected to Honorary Fellowship in recognition of his distinguished record of research in the field of marine zoology and of his 45 years' service as marine zoologist and latterly as Director of the South African Museum; and the following were elected to Fellowship: Guido Mario Dreosti in recognition of his research in food technology and fish processing and his work in organizing and directing the Fishing Industry Research Institute since its establishment in 1947; Louis Franklin Freed in recognition of his research in the fields of social medicine and psychiatry.

The deaths during the year of Dr. E. J. Hamlin (a Member since 1913 and a Fellow since 1922), Professor C. van Riet Lowe (a Member since 1930 and a Fellow since 1933), Dr. E. Leonard Gill (a Member since 1925 and a Fellow since 1929), Dr. J. F. Schofield and Major R. W. R. Rankin are recorded with the deepest regret.

At the end of 1956 the number of Fellows was 91 and there were 215 Members, the highest in the history of the Society, including 31 new Members elected during the year.

Invitations were received to nominate delegates to a number of international scientific congresses. The President, Dr. S. H. Haughton, represented the Society at the XXème Congrès Géologique Internationale held in Mexico in September.

The Index to the Transactions of the South African Philosophical Society and of the Royal Society of South Africa, 1878-1955, edited by A. M. Talbot, Honorary Acting Editor of the Transactions, was published in September. The Council wishes to express the gratitude of the Society to the South African Council for Scientific and Industrial Research for a grant towards the costs of preparing and printing the Index and to Mrs. Talbot and Mrs. Robinson for their work in compiling and checking it.

Part 1 of Volume XXXV of the Transactions was published in August.

From the Society's Library 159 periodicals and 48 books were issued during the year.

The Council gratefully acknowledges the receipt of a number of publications, and wishes to express the appreciation of the Society to the various donors.

The Council also wishes to express the thanks of the Society to the Department of Education, Arts and Science for a grant of £400, to the University of Cape Town for a subvention of £72 7s. 5d. towards publication costs, and to Professor M. H. Giffen and Dr. E. M. van Zinderen Bakker for donations to General Funds.

W. J. TALBOT, *Hon. General Secretary.*

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR JANUARY 1 TO
DECEMBER 31, 1956

EXPENDITURE	£ s. d.
To Petty Cash (Clerical Assistant)	15 4 2½
" Clerical Assistance	60 0 0
" Petty Cash (Treasurer)	10 0
" Stationery	27 1 2
" Printing	11 7 0
" Hire of Hall (La Rochelle; Medical)	4 14 6
" Library, rent and insurance, 1956.. .. .	36 18 0
" Neill & Co. (Insurance)	2 10 0
" University Film Unit	2 2 0
" Wreaths	1 14 10
" School of African Studies (Refund)	1 2 6
" Assistance Compilation of Index	31 10 0
" Legal opinion re Trusteeship Athenaeum.. .. .	8 8 0
" Rustica Press: Provision for Printing and Distribution of Transactions (Vol. 35, pt. 1) and Index	614 12 0
" Bank charges	5 6 3
" Interest as per contra capitalized	105 18 2
" Unappropriated income	199 16 5½
	<hr/>
	£1,128 15 1

INCOME	£ s. d.	£ s. d.
By Subscriptions—1957	7 2 1	
" " —1956	368 9 8	
" " —1955	46 14 2	
" " —1954	1 0 0	
" " —1953	19 11	
	<hr/>	
" Life Fellowship Donations		424 5 10
" Entrance fees		30 0 0
" Sale of Publications and Reprints:		18 0 0
Transactions of the Society	67 4 2	
Wicht Reports	9 10	
Broom Commemorative Volume		
Reproductions	1 4 0	
Costs of Reprints refunded	6 7 2	
	<hr/>	
" Grants:		76 13 8
Secretary for Education	400 0 0	
University of Cape Town	72 7 5	
	<hr/>	
" Interest accrued:		472 7 5
Standard Bank Savings Bank	10 10 0	
P.O. Savings Bank	39 9 7	
C. of G.H. Savings Bank	42 4 10	
Marloth Memorial Fund: (a) Rand Prov. Bldg. Soc. Int. F/D	4 19 2	
(b) U.B.S. Int. F/D	4 7 3	
President's Fund: Int. 1956	4 7 4	
	<hr/>	
" Donations to General Funds		105 18 2
		<hr/>
		1 10 0
		<hr/>
		£1,128 15 1

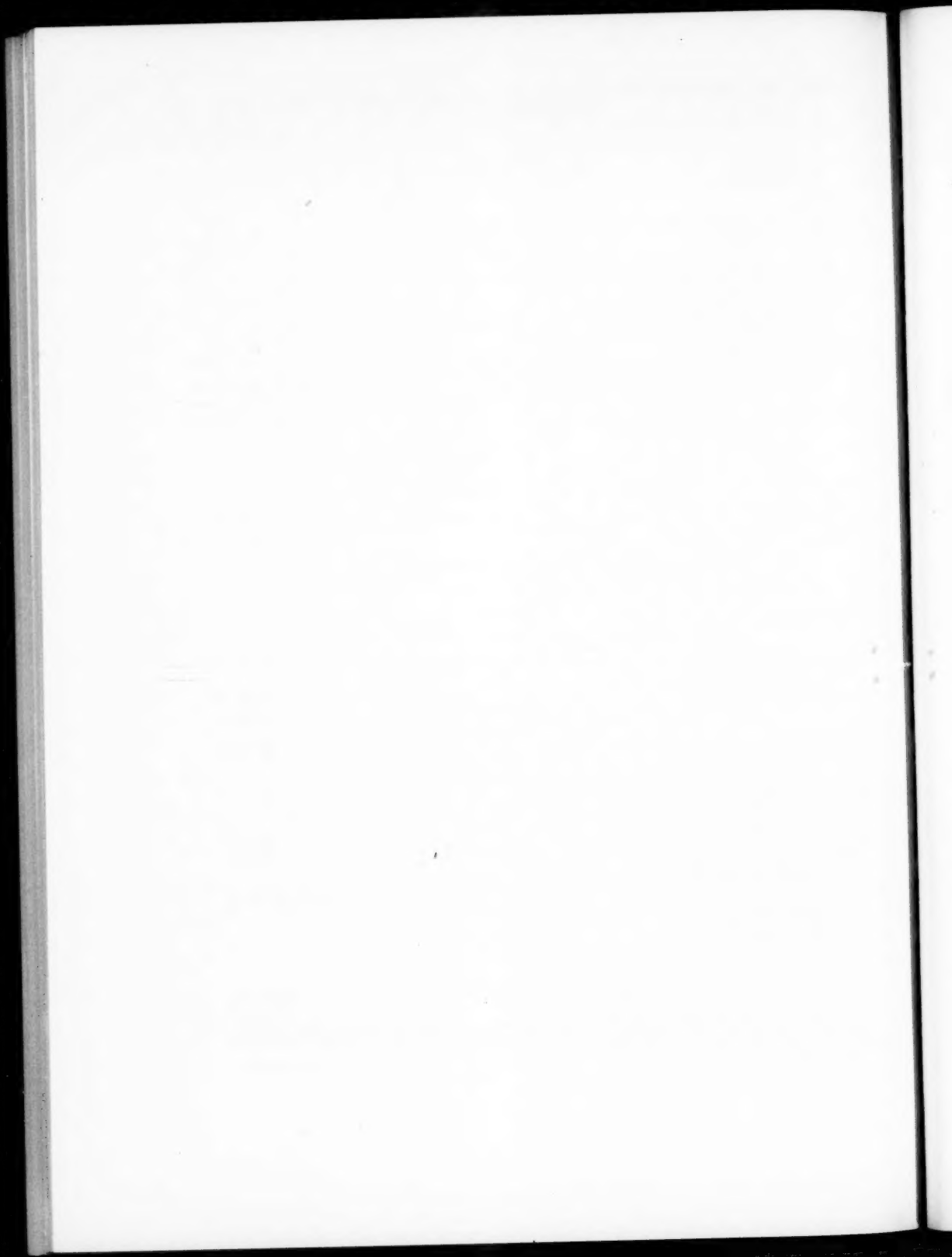
LIABILITIES AND ASSETS AT DECEMBER 31, 1956

[illegible]

We hereby certify that we have examined the accounts of revenue and expenditure, and assets and liabilities, that we have compared them with the books, vouchers and other documents related thereto, and that in our opinion these accounts set forth a correct description of the affairs of the Society.

H. B. RYCROFT }
MARTIN J. POLLARD } *Hon. Auditors.*

N. SAPEIKA, *Hon. Treasurer.*



TRANSACTIONS OF THE ROYAL SOCIETY OF SOUTH AFRICA

Volume XXXV

MINUTES OF PROCEEDINGS, 1957

COUNCIL FOR 1957

President: E. Newbery, D.Sc.

Hon. General Secretary: R. H. Stoy; *Hon. Treasurer:* N. Sapeika; *Hon. Editor of Transactions:* W. J. Copenhagen; *Hon. Librarian:* J. H. Day; *Other Members of Council:* R. Elsdon-Dew, A. J. H. Goodwin, S. H. Haughton, W. J. Lütjeharms, S. M. Naudé, S. H. Skaife, J. M. Watt, Monica Wilson.

REPORT OF THE HONORARY GENERAL SECRETARY FOR 1957

The Anniversary Meeting, the Annual Meeting and seven Ordinary Meetings were held during the year at The Athenaeum, 154 Camp Ground Road, Newlands; the Ordinary Meeting in September was held in the Zoology Department of the University of Cape Town.

The retiring President's address, 'The Geophysicist and Geological Problems', was delivered by Dr. S. H. Haughton at the March meeting.

Other communications read during the year were:

1. 'The family Polyceridae and Goniodorididae (Mollusca Nudibranchia) in Southern Africa', by William Macnae, communicated by J. H. Day. May 15.
2. 'Further notes on Mysidacea from South African waters', by Olive S. Tattersall, communicated by J. H. Day. May 15.
3. 'The benthic ecology of False Bay': Part 1. The biology of infratidal rocks, observed by diving, related to that of intertidal rocks, by J. F. C. Morgans, communicated by J. H. Day. November 20.

Seven lectures were given before the Society:

1. 'Heart sounds', by A. W. Sloan. April 17.
2. 'Optical methods in fluid measurements', by W. Hermann. May 15.
3. 'Modern ideas of nuclear structure', by R. D. Cherry. June 19.
4. 'The Ice Age, African climates and radio-carbon dating', by R. F. Flint. August 21.
5. 'The relation between African and European avifauna', by K. K. Voous. September 18.
6. 'Petroleum as a chemical raw material', by W. F. Hirst. October 16.
7. 'The Cape element of the African floras and the problem of its origin', by M. R. Levyns. November 20.

A pleasing feature of the year has been the number of very successful meetings and other activities held jointly with other scientific bodies in the Cape. Thus the meeting in June was held jointly with the Cape Section of the Royal Institute of Chemistry, that in August with the South African Archaeological Society, and that in September with the Cape Bird Club. In addition the Society acted as one of the sponsors for a very pleasant Science Conversation held at the South African Museum on August 5 and also for the repetition by Dr. H. B. S. Cooke in Cape Town on October 1 of his Alex du Toit Memorial Lecture entitled 'Some observations on the Quaternary and its problems in Central and Southern Africa'.

At the Annual Meeting in October the following were elected to Fellowship:

DR. RAYMOND ALBERT ALEXANDER

in recognition of his contributions to research and studies in virology for vaccine production for the immunization of domestic animals.

DR. JACK JOSEPH FRANKEL

in recognition of his contributions to mineralogical and petrological research in South Africa.

PROFESSOR ISIDORE GORDON

in recognition of his contributions to the medico-legal field both in respect of original work in forensic pathology as well as in his critical review of medico-legal literature.

PROFESSOR FREDERICK GEORGE HOLLIMAN
in recognition of his contributions to stereochemistry.

DR. RAIMUND HILMAR MARLOTH
in recognition of his contributions to citrus and subtropical horticultural research.

The deaths during the year of Miss M. Wilman (a Member since 1898), Professor E. T. Stegmann (a Member since 1917), Mrs. Gordon Bolitho (a Member since 1934), and Professor M. van den Ende (a Member since 1949 and a Fellow since 1953) are recorded with the deepest regret.

At the end of 1957 there were 205 Members and 93 Fellows. There were 239 institutions in 57 different countries receiving the Society's publications either on an exchange or on a subscription basis. Part 2 of Volume XXXV of the Society's Transactions was published in July.

The Council has decided to allot some of the unappropriated income shown on this year's accounts to the purchase of equipment for the meeting room to add to the effectiveness and dignity of the Society's meetings.

The Council wishes to express the thanks of the Society to the Department of Education, Arts and Science for a grant of £400, to the Council for Scientific and Industrial Research, the University of Natal, and the University of Cape Town for subventions towards the cost of publication of papers communicated to the Society, and to Professor Giffen and Mrs. Rankin for donations to the General Funds.

The Council would also like gratefully to acknowledge the receipt of a number of publications and to record the appreciation of the Society to the various donors.

R. H. STOV
Hon. General Secretary

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR
JANUARY 1 TO DECEMBER 31, 1957

EXPENDITURE		INCOME	
	£ s. d.		£ s. d.
To Petty cash (Clerical Assistant)	17 18 5	By Subscriptions: 1959	2 0 0
" Clerical assistance	77 10 0	" 1958	10 1 8
" Petty cash (Acting Editor)	3 18 0	" 1957	375 11 0
" Stationery	31 18 4	" 1956	42 5 11
" Printing	27 1 0	" 1955	8 19 8
" Hire of hall (La Rochelle)	2 5 0	" 1954	1 0 6
" Library, rent and insurance	36 18 0		
" Neill & Co. (Fire insurance)	2 11 9	" Entrance fees	439 18 9
" Wreath: Late M. Wilman	2 2 0	" Sale of publications and reprints:	18 0 0
" Johannesburg Public Library (postage) ..	1 10 6	Transactions of the Society	5 0 6
" Assistance re binding of books (M. Allpass)	13 11 0	Broom Commemorative	
" S.A. Museum (contribution to Con-		Volume	1 4 0
versation)	10 0 0		6 4 6
" Geological Society (contribution to Du Toit		" Grants:	
Memorial Lecture)	5 0 0	Secretary for Education	400 0 0
" Blacher Bros. (filing cabinet)	17 8 0	University of Cape Town	119 4 6
" Rustica Press: printing and distribution of		C.S.I.R.	80 0 0
Transactions (Vol. 35 pt. 2)	371 10 1	University of Natal	25 0 0
" Bank charges	4 9 0		624 4 6
" Interest as per contra capitalized	203 11 0	" Interest accrued:	
" Unappropriated income (part for projector,		Standard Bank (Savings Bank)	54 18 4
lecture apparatus, library index)	463 16 8	P.O. Savings Bank	78 7 6
		C.G.H. Savings Bank	43 19 3
		Marloth Memorial Fund:	
		(a) Allied Building Society	
		Int. F/D	9 13 6
		(b) United Building Society	
		Int. F/D	8 10 2
		President's Fund, Int. 1957	8 2 3
			203 11 0
		" Donation (for General Funds)	1 0 0
	£1,292 18 9		£1,292 18 9

LIABILITIES AND ASSETS AS AT DECEMBER 31, 1957

LIABILITIES			ASSETS		
	£ s. d.	£ s. d.		£ s. d.	£ s. d.
Marlothe Memorial Fund:			Post Office Savings Bank	2,356 2 4	
Capital account as at 31.12.56	287 10 9		Interest	78 7 6	2,434 9 10
Interest, 1957	18 3 8				
		305 14 5	Standard Bank (Savings Bank)	910 10 0	
Life Fund Donations Account:			Interest	54 18 4	
Capital account as at 31.12.56	1,318 4 10				965 8 4
Accrued interest C.G.H.			Standard Bank Fixed Deposit		500 0 0
Savings Bank, 1957	43 19 3		Cape of Good Hope Savings Bank:		
Accrued interest P.O. Savings			A/c No. 86509 (General Fund)		618 16 4
Bank, 1957	15 0 0		A/c No. 79467 (Life Fund)		524 9 1
		1,377 4 1	Marlothe Memorial Fund:		
President's Fund:			Allied Building Society, F/D	139 4 10	
Capital account as at 31.12.56	113 16 1		United Building Society, F/D	121 19 7	261 4 5
Accrued interest (United Building Society)	8 2 3				
		121 18 4	President's Fund:		
Reserve for Publications		1,400 0 0	United Building Society, F/D	104 0 0	
Reserve for Binding		1,500 0 0	Interest	7 16 0	
Capital Account:					111 16 0
Balance at 31.12.56	423 3 6		United Building Society Savings Bank	10 2 4	
Accrued interest:					121 18 4
Standard Bank	54 18 4		Balance at Bank 31.12.57		482 19 0
Post Office	63 7 6		Petty cash on hand		17 6
		541 9 4			
Add Index reserve	500 0 0				
Add unappropriated income ..	463 16 8				
		1,505 6 0			
Less transfer to binding	300 0 0				
		1,205 6 0			
		£5,910 2 10			£5,910 2 10

We hereby certify that we have examined the accounts of revenue and expenditure, and assets and liabilities, that we have compared them with the books, vouchers and other documents related thereto, and that in our opinion these accounts set forth a correct description of the affairs of the Society.

MARTIN J. POLLARD } *Hon. Auditors*
H. B. RYCROFT }

N. SAPEIKA
Hon. Treasurer